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Onions and Other Vegetable Alliums, 2nd Edition

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Preface

A number of people, including lecturers, researchers and seed company staff, have told me that they found the first edition of this book useful. This is the best reward for writing such a book. A lot of new allium science has been published since the first edition and progress has been rapid, particularly in the fields of genetics, plant breeding and plant pathology, where the techniques of molecular biology have had great impact. So, an attempt at an update was clearly worthwhile. Shortly before writing the first edition I had co-edited the multi-author *Onions and Allied Crops* with Haim Rabinowitch, so up to date reviews by experts in the relevant science were to hand and familiar to me. For this edition, I have had to resort more to the original research literature, although the reviews by contributors to Rabinowitch and Currah's (2002) *Allium Crop Science: Recent Advances* were key sources for many topics. A book of this breadth cannot attempt to be an exhaustive review of the research literature and, inevitably, in choosing what research to mention, there is some bias to what I am familiar with, notably towards work from Wellesbourne, from the UK and what is published in English. I apologize to those who have done interesting work which is not mentioned but, nevertheless, I hope the book gives a reasonable overview of the current scientific understanding about the vegetable alliums. I hope this second edition will help to raise and maintain awareness of the huge and continuing achievement of allium scientists in discovering so much fascinating and useful information about these crops. These researchers are the real heroes and heroines behind this book. I hope I have not misrepresented their work by error, omission or misplaced emphasis.

The aim of the book is to introduce the scientific principles that underlie production practices, rather than to give detailed instruction on how to produce allium crops. If the crop technologist has an understanding of the basic principles fundamental to his craft he/she should be better able to adapt his/her methods to changing circumstances and opportunities, and better be able to understand and cope with any abnormal or unusual problems that he/she encounters. Understanding of principles should also improve his/her

judgement in deciding between possible alternative techniques. Furthermore, the details of production methods change as new products, legislation or market conditions arise, whereas the underlying principles remain true and relevant, although of course our knowledge of principles improves and increases as science progresses.

It may seem over-ambitious to cover the wide range of science closely relevant to allium production, but one advantage of such an undertaking is that it reveals connections between different aspects of the underlying science and, sometimes, conflicts in the recommendations for practice coming from them. Furthermore, the crop grower has to embody the integral of all the underlying science in his/her production methods. The book is obviously aimed at students and professionals with a special interest in the allium vegetables, but I hope it might interest the occasional, more general, reader. On my first day as an undergraduate agricultural student at Wye College, UK, I remember the then Principal, Dunstan Skilbeck, remarking in his introductory talk to new students, that the studies they were about to embark on were not only a source of practically applicable information but also offered a 'window' into many fields of knowledge; a possibility particularly well provided for by broadly based courses like agriculture or horticulture. In a more limited way, I hope that this book may serve not just as a source of some rather specialist information on the production of alliums, but can chart a path through many of the disciplines of plant science and show how they connect and interrelate when it comes to application in crop technology. This aspiration might not quite be on a par with William Blake seeing 'a world in a grain of sand', but I hope readers will appreciate that one can see a lot of plant science in an onion.

Crop production has its roots in a pre-scientific era when custom and practice must have evolved 'recipes' for successfully growing crops. Slowly this practical knowledge has become explained, improved and elaborated by connection with the systematically organized and logically connected body of scientific knowledge. There are successive phases in this scientific systematization. First there is observation, description and listing of phenomena. Then there is an attempt to make generalizations and a search for principles that unify a wide number of observations. This usually involves making connections with information from outside the confines of the particular phenomena being studied. If successful, some general principles emerge which can be used to make predictions beyond the original observations. This is when theory becomes not just interesting, but useful, and can begin to feed new methods into production technology. With further advancement and precision of knowledge it becomes possible to explain observations not just in terms of some qualitative general principles, but in numerical terms, i.e. to give quantities to predictions from theory which match subsequent measurements. Such matching of quantitative prediction with observed measurement has been the cornerstone of physical science since Newton's time but, since

the late 1940s, aspects of crop science have become quantitative. Hence, I have included a fair number of models and equations in the text describing various aspects of crop physiology in particular. I hope some readers will not be dissuaded by these, they simply summarize succinctly a lot about the physiological responses concerned. However, the accompanying graphs and verbal descriptions give the gist of what is relevant, so detailed study of the equations is not essential. Such equations are, however, the basis of the computer-based models that are being used increasingly to integrate scientific information so it can be applied in crop management – for example, to forecast irrigation or fertilizer requirements, or to predict disease and pest outbreaks and, therefore, when to apply preventive pesticides. The other major trend of recent years is the increasing application of molecular methods to allium science, particularly to taxonomy, genetics and pathology. These techniques are revolutionizing crop breeding and increasing the rapidity and precision of pathogen identification, and therefore leading to improved diagnosis of crop disease and understanding of disease epidemiology. In a few places I have included a sentence or two in explanation of the background science to give some orientation to readers not already familiar with a topic, mainly to try briefly to explain the purpose and implications of the work being discussed. I hope more expert readers will forgive this occasional dip into what may already be well known to them.

Acknowledgement to those who have helped me produce this book starts with my late father, Leonard K. Brewster, who first got me scratching the soil and sowing seed on the family vegetable plot when I was about 4 years old. Furthermore, he always encouraged enquiry, discussion, debate and clear use of English. I was fortunate enough to take a crop science degree at London University's, now sadly defunct, Wye College. Here, amid the glorious east Kent countryside, I first encountered the excitement of academic enquiry fostered by the wide range of subjects taught in a university agriculture faculty. Discussions with like-minded fellow students kindled interests that have remained with me ever since. Later, from Bernard Tinker, Peter Nye and other mentors in the former Soil Science Laboratory at Oxford, I had the good fortune to be shown how quantitative thinking from the physical sciences was becoming increasingly relevant to the progress of crop science. I thank the former director of Wellesbourne, Professor John Bleasdale, for the opportunity to take up a post to investigate 'what makes onions tick' in an era when funding was available for fairly broadly defined and long-term research in crop physiology. I am grateful to UK taxpayers for funding this work. Working at Wellesbourne, I became acquainted with the research of colleagues in virtually all the scientific disciplines immediately relevant to field vegetable production. Discussions with, and presentations given by, these colleagues inform this book and I hope I have done justice to those aspects of their work reported on here. Among former Wellesbourne colleagues I owe particular gratitude to Dr Lesley Currah, who has drawn my attention to countless

reports on aspects of allium research over the years, the late Mr Harold Roberts for his profound insights on weed science and onion agronomy, and to Professor Duncan Greenwood, whose stimulating discussions on virtually all matters scientific – but in particular about soil–plant relations – have been an inspiration over many years. I thank Warwick University and the current director of Wellesbourne, Professor Simon Bright, for access to the excellent library there, without which I could not have prepared this book, and the library staff there, past and present, for their hospitality and help.

The International Society of Horticultural Science edible allium conferences initiated in Argentina in 1994 by Dr Claudio Galmarini have given me regular updating on the frontiers of research in the subject worldwide. The information so gained, and also by e-mail at other times from allium scientists internationally, has helped me greatly in the preparation of this book. The agricultural science abstracts database of CABI, accessed via Warwickshire College, has been an invaluable resource for systematically reviewing the scientific literature on the allium crops. Thanks are due to my publishers at CABI, formerly Tim Hardwick and latterly Sarah Hulbert, for their patience and cheerful encouragement in the later stages of this work. I thank the editors of this series, Dr Alun Rees and Professor Jeff Atherton, for the invitation to write a second edition and for reading and commenting on draft chapters. I thank Warwick HRI, Wellesbourne and the allied vegetable breeding and seed production companies Bejo Zaden B.V. and de Groot en Slot B.V. of Warmenhuizen and Broek op Langedijk, respectively, The Netherlands, for kindly providing the photographs of pest and disease damage in the colour plates. I thank my friend John Pendleton of Design Principles, Kineton, Warwickshire, UK for donating his time and expertise *gratis* to produce the botanical illustration of vegetable alliums in Plate 1. I am grateful to have learned Maharishi Mahesh Yogi's Transcendental Meditation Sidhi technique so as to be able to take a systematic break from focused mental work to relax and refresh the mind twice a day on a routine basis. Finally, I thank my wife Marnie for inspiring me to undertake a second edition, for her continuous support and encouragement, and for tolerating nearly 4 years of relative neglect of house and garden while I researched and wrote it.

1

The Classification, Origins, Distribution and Economic Importance of the Major Vegetable Crops

The edible alliums include some of man's most ancient cultivated crops, including onion, garlic, leek and Japanese bunching onion. Depictions more than 5000 years old of onion bulbs and models of garlic bulbs have been found in Egypt. The most important cultivated crops evolved from wild relatives that grew in the mountainous regions of central Asia. Many species of wild allium are edible and some are still collected for food, but only a few species are commercially cultivated as food crops and it is with these that this book is mainly concerned. Some of the major crop species are illustrated in Plate 1.

CLASSIFICATION OF ALLIUMS

The botanical classification of alliums, revised according to recent findings using molecular techniques, was summarized by Friesen *et al.* (2006). The genus occupies the following taxonomic context (APG, 2003):
Class Monocotyledones
Order Asparagales
Family Alliaceae
Genus *Allium*

After the Poales, which include the cereal crops, the Asparagales is the second most economically important monocot order. It includes agave, aloe, asparagus, chive, garlic, iris, leek, onion, orchid and vanilla. The Alliaceae are grouped into the 'higher' Asparagales, closely related to the economically important Asparagaceae (asparagus) and the Amaryllidaceae (yucca and other ornamentals) (Kuhl *et al.*, 2004).

There are estimated to be about 780 species in the genus *Allium* (Friesen *et al.*, 2006), with 650 having two or more names (synonyms) (Mathew, 1996; Fritsch and Friesen, 2002).

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Members of the genus *Allium* are perennial, mostly bulbous, plants with:

- underground storage organs: bulbs, rhizomes or swollen roots.
- bulbs often on rhizomes, which can consist of the thickened basal sheaths of leaf blades plus inner, thickened, bladeless 'true scales' or prophylls (as in onion) or of just the thickened, bladeless prophylls (as in garlic) surrounded by several membranous, dry skins.
- rhizomes, which can be condensed or elongated and branched.
- basal leaves arising from the underground stem; the leaves can have long, concentric sheaths forming a false stem or 'pseudostem', as in leek.
- bracts, often fused into a spathe that covers the developing inflorescence.
- flowers borne in clusters of a loose few up to several hundred in a dense inflorescence.
- the individual flowers have a short stalk, are radially symmetrical, have floral parts arranged in groups of three and the carpels develop above the other flower parts.
- the tepals and stamens both occur singly or as two whorls or three, the inner whorl of stamens often being widened at the base; the flower colour is mostly white or rose to violet, and occasionally blue or yellow.
- the ovary has three cells (locules) with two or more ovules per locule; there are often nectaries at the base of the ovary.
- the style is single with a slender, or sometimes slightly swollen, stigma that can have three lobes.
- the seeds are globular to angular and black due to the phytomelan in the epidermis.
- the reserve carbohydrates are fructans, and many species release the breakdown products of cysteine sulphoxides (CSOs) with their characteristic smells (see Chapter 8) although this is often missing, particularly in species of the the subgenus *Melanocrommyum*, to which the largest number of ornamental species belong.
- a basic chromosome number of eight is most common, but seven is found in many of the subgenus *Amerallium*, many of which are native to North America.

Infraspecific classification

The species of the Alliaceae have been grouped into various subgenera and sections based initially on their visible features (Hanelt, 1990). In recent years these groupings have been largely confirmed but refined using molecular techniques, so that the relationships and phylogeny (family tree) of the different species are becoming clearer (Fritsch and Friesen, 2002; Klaas and Friesen, 2002; Friesen *et al.*, 2006).

Over time various processes cause differences in the nuclear, chloroplast

and mitochondrial DNA between different and divergent species to occur and accumulate. Many of these differences have no apparent effect on the form or functioning of the plant and are therefore not subject to evolutionary selection. This pool of information can be used to reconstruct the course of evolutionary divergence without using morphological or anatomical features. In the case of DNA that is expressed in protein synthesis, these changes may be reflected by accumulating differences in the proteins – for example, enzymes between different plants and groups of plants. A number of molecular separation techniques allow these differences to be detected. Such differences for a specific gene or DNA fragment are termed polymorphisms, and forms of the same enzyme with different protein structures, which can be separated by molecular fractionation techniques, are called isozymes. The extent of difference between such polymorphic DNA fragments and isozymes between plants can be quantized and used in measures of difference or divergence between individuals, species and groups of species. Natural selection for a particular ecological situation can sometimes drive unrelated species to a similar morphology or anatomy; this is convergent evolution and can be misleading to those using such observable (phenotypic) features to classify plants and reconstruct their evolutionary path (phylogeny). This problem does not arise when measuring molecular differences that have no phenotypic consequences for the plants being compared.

The Friesen *et al.* (2006) classification is based on differences in the nucleic acid base sequence from the intergenic transcribed spacer (ITS) region of the ribosome DNA from the nucleus of 195 allium species and five species from closely related genera. Their analysis breaks the whole genus *Allium* into 15 subgenera, which subdivide further into 63 sections. The subgenus *Cepa*, which includes onion, is the most divergent or 'advanced' from the related genera outside the alliums. The subgenus *Cepa* along with subgenus *Allium*, which includes garlic and leek, are within a distinct 'advanced' group of common ancestry (clade) that diverges from another group, which includes the subgenus *Melanocrommyum*, some of which are used as ornamentals (Kamenetsky and Fritsch, 2002).

All the above subgenera fall within a larger grouping that is clearly separate from a clade which includes the subgenus *Amerallium*, in which are the North American species with a basic chromosome number of seven. The molecular data show very high 'genetic distances' within the genus *Allium*. These distances are typical of those found between subfamilies or even families in other plants. This suggests that the genus *Allium* is of ancient origin but that molecular evolution has not been accompanied by a great divergence in plant type. The molecular differences, together with the distribution area of alliums, indicate that the genus originated early in the Tertiary geological era, i.e. about 60 million years ago (Friesen *et al.*, 2006).

Rhizomes used to be considered a primitive or ancestral feature in allium classification and the former subgenus *Rhizirideum*, delineated by this feature, included *A. cepa* (onions) and *A. schoenoprasum* (chives). Phylogenetic trees

based on molecular markers indicate that rhizomatous species are not all immediately related and rhizomes must have evolved independently several times, an example of 'convergent evolution'. In the new classification subgenus *Rhizirideum* is a much more restricted group than formerly.

Subgenus *Cepa*

This subgenus of the alliums includes: (i) the section *Cepa*, to which belong the major crops onion, *A. cepa* and Japanese bunching onion, *A. fistulosum*; (ii) the section *Schoenoprasum*, to which the chive, *A. schoenoprasum* belongs; and (iii) the section *Sacculiferum*, to which the oriental crop rakkyo, *A. chinense* belongs. Plants in this subgenus have slender, hollow leaves and short, vertical rhizomes, an extreme example of which is the disc-like baseplate of onion.

SECTION *CEPA* This small group, which includes onion and Japanese bunching onion, has cylindrical, opposite leaves and bulbs formed from several leaf bases covered by thin, dry skins. The leaf sheaths form a pseudostem that surrounds the hollow flower scape. Axillary daughter bulbs form tufts or short rhizomes; a progressive reduction of rhizomes within the section culminates in the baseplate disc of onion.

These species occur mainly in the Tien Shan and Pamir-Altai mountains of central Asia. They grow in open rocky sites with shallow soil and have a fairly long annual growth period from spring to autumn, although in arid areas they may show weak summer dormancy induced by drought. They have a long juvenile phase of 3 to 10 years before flowers are produced. Some of the localized species are in danger of extinction, partly because of over-collection for food by local people. It is important that these species do not disappear, as they might contribute valuable genes to the crops (Kik, 2002). The section has been divided into four alliances of closely related species (Fritsch and Friesen, 2002). The *Cepa* alliance includes *A. cepa*, the common onion, *A. vavilovii* and *A. asarense*; *A.vavilovii* is completely interfertile with onion (Kik, 2002) and is an endangered species. The *Altaicum* alliance includes *A. altaicum* and *A. fistulosum*, the Japanese bunching onion.

DISTRIBUTION AND ECOLOGY

The alliums are distributed widely through the temperate, warm temperate and boreal zones of the northern hemisphere. In tropical areas they are confined to mountain areas. In Eurasia the region of greatest species diversity ranges from the Mediterranean eastwards into the mountains of central Asia, through northern Iran, Afghanistan and Pakistan, Tajikstan, the Tien Shan mountains of Kyrgyzstan and north-east China, into the mountains of Mongolia and southern Siberia. The most important crops originated in this centre of diversity (see below). A lesser centre of diversity occurs in western

North America.

Typically, alliums are plants of open, sunny, dry sites in fairly arid climates. Many species are found in steppes, dry mountain slopes, rocky or stony open sites or summer-dry, open, scrubby vegetation (Hanelt, 1990). They are weakly competitive and therefore are not normally found in dense vegetation. However, some woodland species exist – for example, *A. ursinum* and also some pasture species and important weeds, including *A. vineale* and *A. carinatum*.

The annual pattern of growth (phenology) varies widely. Depending on species, flowering can occur in spring, summer or autumn and the growth and development period can vary from 2–3 months in spring to early summer to several cycles per year of leaves or even continuous leaf formation. They can be short- or long-lived perennials. Species of summer-dry regions may show summer dormancy, whereas there are also winter-dormant types adapted to cold regions. Some species from arid regions have only a short growing season in spring and early summer. The crop species have a high nuclear DNA content (see Chapter 3) and fructans as their reserve carbohydrates (see Chapter 8), both features of plants that grow by rapid cell expansion in the cool temperatures of late winter and early spring (Hendry, 1993).

THE TYPES, HISTORY AND EVOLUTION OF THE EDIBLE CROPS

The names and taxonomic grouping of the edible alliums important in commerce are shown in Table 1.1 The seven main food crop species are easily distinguishable, and Table 1.2 and Fig. 1 show features that can be used in identification of these crops.

Table 1.1. Groupings within the genus *Allium* that contain the major crops (from Table 1, Friesen *et al.*, 2006).

Subgenus	Section	Species	English crop name
Butomissa	*Butomissa*	*A. tuberosum*	Chinese chives
Allium	*Allium*	*A. sativum*	Garlic
		A. ampeloprasum	Leek, kurrat, great-headed garlic, pearl onion
Cepa	*Schoenoprasum*	*A. schoenoprasum*	Chives
Cepa	*Cepa*	*A. cepa*	Onion, shallot, multiplier or potato onion
		A. fistulosum	Japanese bunching onion
		A. oschaninii	French grey shallot
Cepa	*Sacculiferum*	*A. chinense*	Rakkyo

Table 1.2. Characters useful in identifying the vegetable allium crops (modified from Table 1.2, Jones and Mann, 1963).

Species	Diploid chromosome number	Storage organs	Time of flowering	Flower colour	Order of opening of florets in umbel	Bulbils in inflorescence
Common onion, *Allium cepa* (including shallot)	16	Foliage leaf bases and swollen, bladeless inner sheaths	Spring to early summer	White, green striped	Irregular	Absent in most cvs
Garlic, *A. sativum*	16	Swollen, bladeless sheaths (cloves); no storage in foliage leaf bases	Spring (or non-flowering)	Lavender to white-green (flowers almost always abort)	Irregular	Always present
Leek and kurrat, *A. ampeloprasum*	32	Bulbs normally absent	Spring to early summer	White to purple	Irregular	Sometimes present
Great-headed garlic, *A. ampeloprasum*	48	Cloves like garlic, but of two sizes	Spring	White to purple	Irregular	Usually absent
Japanese bunching onion, *A. fistulosum*	16	Foliage leaf bases, bulbs absent	Spring to early summer	Pale yellow to white	From apex to base of umbel	Absent in most cvs
Chive, *A. schoenoprasum*	16, 24 or 32	Foliage leaf bases, bulbs absent	Spring and summer	Purple, rose or rarely white	From apex to base of umbel	Rarely present
Rakkyo, *A. chinense*	16, 24 or 32	Swollen foliage leaf bases, bulbs prominent	Autumn (after summer dormancy)	Rose-purple	Irregular	Absent
Chinese chive, *A. tuberosum*	32	Rhizomes; bulbs absent	Mid- to late summer	White	Irregular	Absent

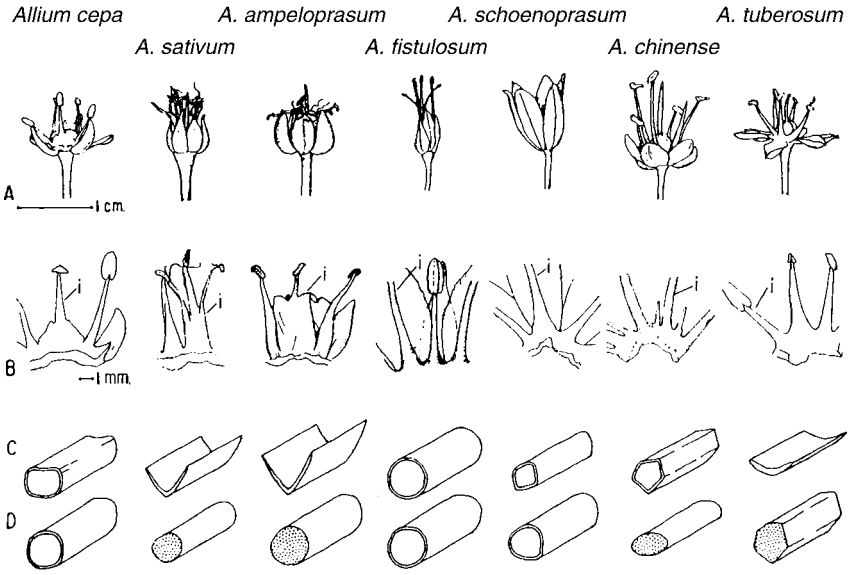

Fig. 1.1. Features used for identifying food alliums. Flowers (A), stamens (B) ('i' indicates the inner stamens) and cross-sections of leaf blades (C) and of flower stalks (D). Leaf and scape sections are not to scale (from Jones and Mann, 1963, Fig. 3. Reproduced by courtesy of John Wiley & Sons Inc.).

Onion and shallot, *Allium cepa* L.

The onion has been cultivated for 4700 years or more and does not exist as a wild species. Onion was probably first domesticated in the mountainous regions of Turkmenistan and north Iran bordering the ancient advanced civilizations of the Near East (Sumerian). Therefore, south-west Asia is regarded as being the primary centre of domestication and variability. Other regions of great diversity like the Mediterranean are considered secondary centres (Hanelt, 1990; Fritsch and Friesen, 2002). The nearest wild relative in the subgenus *Cepa* section *Cepa* is *A. vavilovii* (Klaas and Friesen, 2002), which is found in the Koppet Dag mountains of Turkmenistan. It has a hollow scape with a bubble-like swelling, but the leaves are completely flat. Recent molecular studies have shown that *A. asarense* is basal to the group, which includes *A. cepa* and *A. vavilovii* (Fritsch and Friesen, 2002). This has only very recently been discovered at a single site in the Elburz range near Tehran. It grows on steep, rocky slopes and the plants have semi-cylindrical leaves and a flower stem with a bubble-like inflation. It has globose umbels of greenish brown-tinged flowers.

Hanelt (1990) describes how domestication of onions may have originated as illustrated by *A. pskemense*, another wild, large-bulb species of the section *Cepa*. This grows in the western Tien Shan mountains of Uzbekistan and Kazakhstan, and inhabitants of some valleys transplant it to their gardens where it is cultivated and propagated. During domestication of onions, selection for faster growth, leading to a biennial rather than a longer life cycle, and for larger bulbs must have occurred. Also, barriers to crossing with related species must have developed.

Cultivated types of *A. cepa* fall into two broad horticultural groups, the Common Onion group and the *Aggregatum* group (Hanelt, 1990).

The Common Onion group constitutes the vast bulk of the economically important varieties. These form large, single bulbs (see Plate 1) and are mostly grown from seed. Varieties grown for salad onions and as small bulbs for pickling are mainly from this group. There is great diversity in adaptation to photoperiod and temperature, in bulb storage life, dry-matter content, flavour and skin colour. Many of these aspects are discussed in more detail in later chapters and in the section on onion cultivars below.

The bulbs of the *Aggregatum* group are smaller than the common onion because they rapidly divide and form laterals, hence forming clusters of bulbs. Jones and Mann (1963) distinguished two bulb-forming subgroups: multiplier, or potato, onions and shallots (see Plate 1). Multiplier onions divide into between three and 20 bulbs that are wider than they are long, and which are encased by the dry, outer bulb skins. Shallots form clusters of narrow, separate bulbs, and the leaves and flowers are usually smaller than those of common onions. The *Aggregatum* group is usually vegetatively propagated but, recently, improved seed-reproduced varieties of shallots have been bred and are being widely grown in Europe, Israel and North America. Hybrid cultivars have been developed in Israel and Holland using cytoplasmic male sterility (Rabinowitch and Kamenetsky, 2002). There has, however, been some dispute as to whether such seed-reproduced cultivars truly constitute shallots from the producers of traditional, vegetatively propagated varieties in France.

When flowers form, they are interfertile with the Common Onion group, and therefore they are the same species. In view of this, the specific name *A. ascalonicum*, used for shallots in the past, is not justified. The *Aggregatum* group are not so important commercially as the Common Onion group, and many are grown as home garden crops; however, large-scale cultivation of shallots takes place in Europe, North America, Argentina and in some tropical regions. In France they are favoured for their special flavour and cooking quality as compared with common onions. Vegetatively propagated onions like multiplier or potato onions are traditionally grown in Finland and northern Russia (Aura, 1963). Shallots are also suitable for such high-latitude regions with a short growing season.

Interestingly, at the other extreme of the latitude range, in the humid tropics – particularly in lowland coastal regions, shallots and multiplier onions

are again found to be the most satisfactory way of producing *A. cepa* bulbs (Currah, 2002). In these conditions, pressure from pests and diseases causing leaf damage is intense, and shallots and multiplier onions can complete a cycle of leaf growth and bulbing in 60–75 days, whereas onions grown from seed need a longer season of leaf growth, during which they are vulnerable to pest and disease attack (Currah and Proctor, 1990). Furthermore small seedlings, unlike larger, vegetatively propagated plants, lack the reserves to recover from leaf damage.

Onion cultivars

Because onions have been cultivated for so long, and because their bulb and inflorescence development must be closely adapted to the temperatures and photoperiods that prevail where they are grown, there exists a huge range of cultivars and landraces, developed over the centuries to fit the diverse climates and food preferences of the world. Onions show particular diversity in the eastern Mediterranean countries, through Turkmenia and Tajikistan to Pakistan and northern India and these regions are, therefore, important sources of genetic diversity (Astley *et al.*, 1982). Modern varieties sold by international seed companies – in particular F_1 hybrids, which have a narrow genetic base – are supplanting these old varieties, with a danger that these latter, and therefore the many potentially valuable and adaptive genes they contain, will be lost. This problem, common to many crop species, is termed 'genetic erosion'. Hence, the characterization and collection, preservation and regeneration of seeds and vegetative clones of these old varieties and landraces is very important, and a network of 'gene-banks' concerned with this task has been established (Astley, 1990).

Broadly speaking, several phases of cultivar development have occurred. First, there must have been the original domestication from a wild bulbing species, similar to the utilization of *A. pskemense* described above. Then onion seeds or bulbs must have spread through travel and trade and slowly became adapted to each region to which they were carried. Onion was a common cultivated garden plant in the Greek and Roman Empires. The Romans are thought to have taken the onion into northern Europe and onion was widely cultivated throughout Europe during the Middle Ages. Onion was probably introduced into Russia during the 12th or 13th century. Europeans first took onions to the Americas starting with Columbus. Settlers carried onions from Europe into North America in the early 1600s. Europeans introduced bulb onions to East Asia during the 19th century.

The development of a commercial seed trade with the deliberate selection, testing and introduction of improved varieties was the next phase. Magruder *et al.* (1941) give examples of 18th- and 19th-century seedsmen who introduced onion cultivars to the USA. Development of new cultivars by seed companies continues today. Beginning in the 19th and early 20th centuries, onion development and breeding began in state-funded agricultural experiment stations in

many parts of the world, most notably in certain states of the USA. This work has had a huge impact through the development of F_1 hybrid cultivars (see Fig. 3.5), based on the discovery and exploitation of male sterility genes by Henry Jones and his colleagues at the University of California at Davis (Jones and Clarke, 1947). In the breeding of new varieties in state-funded institutions the systematic exchange and exploitation of genetic material on a global basis has been scientifically documented (e.g. Corgan, 1988). Goldman *et al.* (2000) give the history of publicly funded onion breeding programmes in the USA, including the pedigrees of the resulting cultivars. In recent decades public funding, coordinated by the International Board for Plant Genetic Resources (IBPGR), has been directed toward collecting, characterizing, documenting, conserving and distributing the world's diverse heritage of onion varieties (Astley, 1990). This in turn is facilitating the worldwide exchange and utilization of genetic material in both publicly and privately funded onion breeding.

The successive stages of cultivar development are well illustrated by the progress of the early-maturing, sweet onion crop of the extreme south of the USA. In the late 19th and early 20th centuries, flat-shaped, sweet, short-storing onions, known as Bermuda types, began to be grown in southern Texas. These were of Italian origin (Magruder *et al.*, 1941). In 1925, seed of a short-day, early-maturing, sweet, short-storing Babosa type onion, grown as an overwintered crop on the Mediterranean coast of Spain, was imported from the Valencia region into the USA. This was selected at the New Mexico Agricultural Experiment Station to produce a round top-shaped, thin-skinned, mild-flavoured, sweet variety which was named 'Early Grano'. This cultivar was higher yielding than the Bermuda types and began to supplant them after its introduction.

From this variety the cv. 'Texas Early Grano' was bred at the Texas Agricultural Experiment Station and released in 1944. Resistance to the soil-borne disease pink root (see Chapter 5) was transferred from resistant Bermuda types by crossing and selection. A whole series of Texas Grano-type onions, differing slightly in maturity date, has since been developed at the Texas A&M University, so that a succession of maturity dates between March and May can be achieved in the Rio Grande Valley. These were developed from a cross of cv. 'Texas Grano' with the later-maturing Israeli cv. 'Ben Shemen', itself derived from the Californian cv. 'Sweet Spanish' (Pike *et al.*, 1988).

Similarly, in other parts of the world with mild winters, such as Israel and the Mediterranean coast of Spain, different seasonal cultivar groups mature successively from early spring through the summer to maintain fresh bulb supplies over a long season. In the USA in the mid-1950s H.A. Jones developed the hybrids of the Granex series, starting with cv. 'Yellow Granex', by selection from 'Texas Grano' and incorporation of cytoplasmic male sterility (see Fig. 3.5). Yellow, red and white Granex hybrids are now available and they are among the most widely grown cultivars, since they produce high yields at tropical latitudes. However, as a consequence of their ancestry and their original purpose as an

early-season, non-stored onion, they have thin skins, low dry-matter content, soft flesh and only short dormancy (Currah and Proctor, 1990).

Onion cultivars are distinguished and characterized by a range of features. These have been systematized by IBPGR and are incorporated in their system for classifying cultivar collections (Astley *et al.*, 1982). Distinguishing features of the foliage include the colour (i.e. the depth of green), leaf length and leaf erectness. Bulb features include the bulb shape, the uniformity of bulb shape and the bulb skin colour. Bulb shapes can be globe, a flattened globe, sometimes with a flat top, spindle-like or almost cylindrical. Sometimes there is a high 'shoulder' to the bulb. Skin colours can be white, yellow, light brown, brown, dark-brown, red, purple or green. Features of the inflorescence include its fertility, the flower number in the umbel, the tepal and anther colour, the presence or absence of bulbils (see Fig. 4.41) in the inflorescence and whether an inflorescence is indeed produced or whether reproduction is normally vegetative.

The above features are strongly heritable and easily seen by eye, although many are subject to environmental variability, as has been shown for bulb shape, which is influenced by the population density at which plants are grown (Dowker and Fennell, 1974). Ideally, bulb shape and many other properties important in characterizing a cultivar should be judged by comparisons with standard varieties grown in the same conditions, thereby discounting the effects of environment. Cultivar features characterizable in such trials include bulb skin thickness, the extent of bulb doubling (i.e. how many obvious 'centres' exist when the bulb is sliced transversely), firmness of bulbs, dry-matter percentage in bulbs, sweetness and flavour strength of bulbs, potential storage life and bulb flesh colour. Bulb flesh colours can be white, white-flecked green, yellow, red or purple.

The day-length requirement for bulbing can be judged from the location where the cultivar is grown and the time of year it bulbs. Also, in trials at one location, an indication of day-length response can be gained by comparing the rates of bulbing and maturing of different cultivars (e.g. Magruder *et al.*, 1941). Features of flowering that are characterized in comparative trials include the length of the scape, the time of flowering relative to standard varieties and the cold requirement for bolting, usually measured as percentage of bolting relative to a standard variety. Features of great practical significance, and which again require comparative screening against standard varieties, include susceptibilities to pests and diseases and ability to tolerate soil or climatic stresses. Organs not selected for by humans – for example, the flower and seed capsule – have been little affected by domestication and exhibit no great variation (Fritsch and Friesen, 2002).

In the catalogues of seed companies that trade over a wide geographical area onion cultivars are frequently classified into 'short-day' (SD), 'intermediate-day' (ID), 'long-day' (LD) and 'very long-day' (VLD) day-length types. This refers to the minimum day-length (photoperiod) needed to stimulate bulb development. LD types are characterized by long-storing cultivars from the north-eastern USA and

VLD types are typical northern European long-storing cultivars. Within these groupings smaller differences in day-length response give early, maincrop and late cultivars. Very approximately, short-day onions can initiate bulbs when day-lengths exceed 11–12 h, intermediate-day types when day-lengths exceed 13–14 h and long-day types require > 16 h. Careful experimentation shows these criteria to be subject to much qualification (see Chapter 4); however, the division of cultivars into these broad response groups gives a general indication of their suitability for bulb production in different regions.

Short-day onions can produce bulbs at low latitudes where photoperiods remain close to 12 h throughout the year, although many varieties widely used in the tropics were bred for autumn sowing as early spring-maturing crops at higher latitudes – for example, the Texas Early Grano types discussed above. Intermediate-day varieties are typically grown at middle latitudes as over-wintered crops, and they begin to bulb in the spring ready for harvest in the late spring and early summer. Long-day varieties are typically sown in the spring at high latitudes and bulb in the mid- to late summer. If a cultivar has an inappropriate day-length response for a locality it is useless for bulb production. For example, a long-day variety growing at near equatorial latitudes will not bulb at all, since photoperiods do not reach sufficient length to stimulate the process. On the other hand, a short-day variety sown in spring at high latitudes will be stimulated by long photoperiods to bulb almost as soon as leaves have emerged. Consequently, bulbs will develop on tiny plants and will be very small.

Molecular techniques are now being applied to investigate the relatedness of onion cultivars. Analysis of simple sequence repeats, SSRs, in the DNA of 35 different cvs of diverse origin yielded a 'family tree', with cultivars grouped into well-defined categories (Jakse *et al.*, 2005). LD storage cvs from the USA were closely related to those from Japan, consistent with the introduction of these types of onion to Japan from the USA. European LD storage types formed another cluster more closely related to a cluster of SD and ID short-storage cvs than to US and Japanese LD storage types.

Bark and Havey (1995) investigated genetic diversity in 17 open-pollinated populations of onions that bulb in short days (SD) and long days (LD) using RFLP polymorphisms probed by random complementary DNA. One hundred and forty-six polymorphic DNA fragments were scored for presence or absence and the data were used to calculate how closely related each population was. The populations did not clearly separate according to the day-length response. The SD populations were genetically more diverse and it appeared that the more uniform LD populations were derived from them. SD onions may show greater genetic diversity because they have been maintained as landraces and open-pollinated cultivars over a wide geographic area, whereas intermediate and long-day cultivars are more localized (Currah, 2002).

There is now a danger of diversity in the SD gene pool being lost because new hybrids and highly bred, open-pollinated cultivars from international seed companies are replacing traditional cultivars in tropical areas.

Because of the widespread intercrossing and breeding of new cultivars that is continuously occurring, there is little point in drawing up formal classification schemes for grouping varieties. Each country or region tends to have its traditional varieties, so any discussion of specific cultivars is inevitably highly selective. Here, a few particular cultivars which have been important in breeding or world trade will be discussed to illustrate some important types of onion and to show the background to their development.

In the USA three broad classes of fresh-market onions are produced. The southernmost states produce the autumn-sown, early, sweet cultivars, the development of which has been discussed above. In the western mountain states cv. 'Sweet Spanish' and similar types are sown in late winter to produce large, mild, sweet bulbs in August and September. These types can be stored for several months. In the north and north-east of the USA long-day cultivars are grown, which are hard, pungent and long-keeping. Dehydrated onions are also an important product in the USA and both the long-day cv. 'Southport White Globe' and the short-day cv. 'White Creole' were developed to have the white skins, white flesh and high dry matter content that are ideal for dehydration and processing to produce onion flakes and powder (Jones and Mann, 1963). The California-bred cv. 'Southport White Globe' is grown for processing in many other parts of the world including Spain, New Zealand and Argentina (Bosch-Serra and Currah, 2002). In the USA hybrid cultivars are increasingly used, but open-pollinated, non-hybrid varieties persist, particularly where transplants are grown e.g. southern Texas. The obvious advantages of hybrids to seed companies are that they keep control of the parent lines and varieties do not breed true from farmer-saved seed.

In north-western Europe the dominant cultivars are mainly similar to, and developed from, the old Dutch Rijnsburger type. Their bulbs are globe-shaped, yellow- to brown-skinned, firm, pungent and long-storing. In recent years F_1 hybrids have constituted an increasing proportion of this type of onion. Of the cultivars of spring-sown bulb onion listed by the National Institute of Agricultural Botany (NIAB) in the UK, five out of 17 were hybrids in 1982, whereas in 1992, 19 out of 21 were hybrids (NIAB, 1982, 1992).

Spanish onions have long been renowned as an export crop to northern Europe. The firm-fleshed, round, long-storing 'Grano' type onions are harvested in July and August and produce a high-quality crop. Many cultivars which have become important in other parts of the world derive, at least in part, from this type, including the remarkably long-storing cv. 'Pukekohe Long Keeper' of New Zealand (Grant and Carter, 1986) and its Australian derivative, cv. 'Creamgold'.

The main types of onion suitable for growing in temperate and Mediterranean climates were tabulated by country within each continent by Bosch-Serra and Currah (2002). This list names particular cultivars of each type and highlights features which are important for the markets served, e.g. bulb shape, colour, storability, etc. These authors also include a table, based on the work of Tarakanov, which describes similar features for cultivars grown in Russia and territory of the former USSR.

Currah (2002) gives tables listing the names of cultivars grown in countries of tropical and subtropical Africa, Asia, the Americas and the Caribbean. The yields and storage performance of these cultivars are listed by Currah and Proctor (1990). Onion cultivars developed for early-spring bulbs in southern Texas and California are widely grown in tropical countries, as these cultivars can produce large bulbs in the short day-lengths of equatorial regions – for example, the hybrid cultivars 'Granex 33' and 'Granex 429'. These onions grow vigorously, produce large, single-centred bulbs, are mild-flavoured, juicy and low in dry matter, have thin skins and a short storage life (< 2 months) under ambient tropical conditions. A number of US seed companies market cultivars of this type throughout the tropical world. More recently, breeders in Israel and Australia have developed cultivars suitable for tropical production which are longer storing and have better skin quality, by introducing genes for these properties from long-day genotypes.

Many indigenous tropical varieties still exist as landraces of farmer-saved seed. These may show considerable variation in size, shape and colour within the population. Selection for greater uniformity has stabilized some open-pollinated named cultivars – e.g. 'Poona Red' (India) and 'Red Creole' (Louisiana) – and selection continues to produce new or more highly bred, open-pollinated cultivars. The Creole onions probably originated in the western Mediterranean but have been grown in Louisiana for more than 150 years. They are fairly slow growing but produce pungent, high dry-matter bulbs with tough skins typically able to store for 4–5 months in the tropics (Currah, 2002). They are widely grown throughout the tropics. In the late 1990s a Dutch company (Bejo) introduced cultivars selected from the Indian cultivar 'Bombay Red', and a US company (Asgrow) introduced cultivars selected from West African and Brazilian material. These cultivars aimed to supply tropical consumers with improved medium-sized, pungent red onions (Currah, 2002). Hybrid shallots for growing from seed in tropical regions have also been introduced recently by the Dutch company Bejo.

Japanese bunching onion, *Allium fistulosum* L.

The Japanese bunching onion was historically the main allium vegetable of China and Japan, where it has been cultivated for more than 2000 years, and it remains very important there. While growing, the Japanese bunching onion is very similar in appearance to the common onion, but it does not form dormant bulbs. Further distinguishing features between the two crops are given in Fig. 1.1 and Table 1.2.

Allium fistulosum is not known as a wild species, but *A. altaicum*, a wild relative, is widespread in the mountains of northern and central Mongolia and southern Siberia, somewhat east of where the wild relatives of the common onion are centred. *Allium altaicum* forms bulbs with a fibrous, net-like skin that are

collected for food. *Allium fistulosum* was probably selected from *A. altaicum* in northern China near the southernmost border of its natural area. Interspecific hybrids between *A. altaicum* and *A. fistulosum* have high pollen and seed fertility.

Japanese bunching onions have been grouped into four major types: the 'Kaga', 'Senju', 'Kujyo' and 'Yagura negi' groups (Inden and Asahira, 1990). The first three of these groupings correspond to cultivars adapted to the coolest, intermediate and warmest regions of Japan, respectively. The differences between groups that make them suitable for cultivation in contrasting climatic zones lie in their degree of winter dormancy and their growth rate under low temperature. Kaga types, being adapted to cold regions, become dormant in the winter and grow very slowly at mean air temperatures of around 5°C, whereas the Senju and Kujyo groups grow actively in cool conditions, the growth rate being faster for the latter than the former, and they do not become winter dormant. The Kaga group is grown to produce thick, blanched pseudostems since they form large leaves and do not branch readily. Long pseudostems and blanching are promoted by repeatedly earthing-up as the plants grow. The Senju group is similarly cultivated to produce long, blanched pseudostems. They are grown in central Japan, near Tokyo. The Kujyo group branch easily and are mostly grown for tender, green leaves, although some cultivars are used for blanched pseudostem production in southern Japan. Yagura negi is a home garden crop that produces numerous bulblets and shoots atop its flower stalk. It is winter dormant and is grown to produce edible green shoots in spring and summer. It tillers readily and is propagated by offshoots.

Garlic, *Allium sativum* L.

Garlic (see Plate 1) is thought to have evolved from wild ancestors in a broad area of central Asia stretching from the Tien Shan mountains in the east to the Caucasus in the west. Some authorities consider that *A. longicuspis* is a separate species from which garlic evolved, but others consider that *A. longicuspis* is a wild or feral form of garlic (Fritsch and Friesen, 2002). *Allium tuncelianum* has also been suggested as an ancestor of both garlic and *A. longicuspis*. It smells like garlic and has similar floral morphology, but it is a non-bulbing species. The natural habitat of ancestral garlic was probably gullies and rocky valleys where some water was available, in arid or semi-arid areas. Garlic bulbs in summer and can therefore survive periods of extreme dryness as a dormant bulb. It is also very cold-hardy. Fritsch and Friesen (2002) divided garlic into several informal cultivar groups:

- the *Longicuspis* group of Central Asia, which bolt and some of which are still seed fertile and which also produce many small top-sets.
- the *Sativum* group from the Mediterranean, which includes bolting and non-bolting types.
- the *Ophioscorodon* group from central and eastern Europe, which bolt and produce long, coiling scapes with few large top-sets.

- the *Pekinense* group of China, which are derived from the *longicuspis* group but are smaller and produce a few large top-sets.
- the *Subtropical* group from India, Vietnam and Myanmar, which have small bulbs and are selected for eating as fresh leaves.

A number of authors have proposed alternative classifications based on comparisons of morphology, growth pattern and, in several cases, isozymes or other molecular markers (Etoh and Simon, 2002). Most schemes are broadly compatible with the above groupings but include more detailed subgroups within some of them. Several authors report that the greatest polymorphism in genetic markers is found within the central Asian *Longicuspis* types, and fertile flowers and seed production have been found within this group only (Etoh and Simon, 2002). Within the last 20 years a number of these fertile garlic accessions have been collected in central Asia. Following pollination and removal of top-sets seeds have been produced, of which 12% have germinated (Etoh and Simon, 2002). This has opened up the possibility for improvement of garlic worldwide, using seed reproduction and selection to introduce useful traits from the central Asian centre of origin of the crop.

Garlic clones exist that are adapted to many ecological zones through their responses of growth and bulbing to temperature and photoperiod, their cold-hardiness and duration of bulb dormancy (Takagi, 1990). Diversity also exists in the size of cloves, their number, bulb weight, colour and number of outer skins and size and vigour of the foliage, and the extent to which inflorescences occur. On the basis of a comparison of a wide range of clones growing in a standard environment, Jones and Mann (1963) concluded that there was no justification for using some of the subspecies names previously ascribed to some variants of garlic. They suggested that the name 'Rocambole' might be applied to variants with coiled scapes, but should not be applied to the wild species *A. scorodoprasum*. This has occasionally been so named and it has been used for food but it is not cultivated. Messiaen *et al.* (1993) compared the garlic varieties grown in all parts of the world, except Asia, in comparative trials in France and classified them into six groups characterized by the presence or absence of flower stalks, the size and number of the cloves and their degree of dormancy, and the earliness of bulbing in the trials.

Leek, kurrat, great-headed garlic and pearl onions, *Allium ampeloprasum* L.

This species includes several distinct crop types (see below), but where they have been crossed they have proved interfertile and are therefore variants of the one species. Wild *A. ampeloprasum* is found from Portugal in the west through the Mediterranean countries to western Iran in the east (van der Meer and Hanelt, 1990; Kik, 2002). It grows wild in open, often man-made,

habitats, on cliffs and in scrubby vegetation. The wild types produce small bulbs, either close to the mother bulb or, in some variants, on short stolons. Wild relatives have been successfully crossed with cultivated leeks (Kik, 2002).

There are five horticultural groups: the Leek group, the Kurrat group, the Taree group, the Great-headed Garlic group and the Pearl Onion group.

In leeks the development of concentric, ensheathing leaf bases has been selected so that they form long, edible 'pseudostems' at harvest (see Plate 1). Different types vary in the length and slenderness of the pseudostem. Turkish and Bulgarian types have long, thin pseudostems, whereas those from Western Europe have shorter, thicker pseudostems (van der Meer and Hanelt, 1990). Leeks do not normally bulb but, after flowering, bulb cloves frequently form in the leaf axil at the base of the flower stalk. Leeks are tetraploids with a chromosome number of 32. The flowers have light purple tepals and are produced in globose umbels. Leeks are an important crop in Europe. They are raised from seed. They are well adapted to growing in cool conditions and are harvested throughout the winter in maritime countries of Western Europe. Many of the older cultivars of Western Europe are being supplanted by newer, mainly Dutch-bred, cultivars, including hybrids, which have been developed since the 1990s (Smith and Crowther, 1995). Because leeks, in contrast to onions, do not have specific photoperiod requirements for development, varieties can be grown over a wide range of latitudes. The name *A. porrum* was given to leek by Linnaeus, and this name is still quite widely used.

In kurrat the emphasis of selection has been for edible leaves, and the pseudostem is quite short. The crop is popular in Egypt where the leaves are repeatedly cut and harvested every 3–4 weeks over a period of up to 18 months. It is grown from seeds and is tetraploid, like leek, with which it is easily crossable to give morphologically intermediate and fertile offspring. The Taree group, which is sometimes included in the Kurrat group, is a narrow-leafed form cultivated as a leafy condiment in northern Iran.

Great-headed garlic has the appearance of a very robust garlic plant. It produces a large, leek-like inflorescence, but any seeds produced are sterile and it rarely forms top-sets in the inflorescence (Jones and Mann, 1963). It is therefore propagated from the cloves, which are like large garlic cloves. Six large cloves typically surround the base of the flower stalk, sometimes with smaller cloves encased in the wrapper leaves of the bulb. If the plant does not flower, the bulb consists of a single, large clove, termed a 'round'. Great-headed garlic is hexaploid, with a chromosome number of 48. The flavour is similar to that of garlic (see Table 8.1) and it is often confused with garlic by gardeners. Cultivation is reported from Greece and Egypt and through south-west Asia to India, often on a small scale.

Pearl onion is a minor, home-garden crop in Germany which has, in the past, been grown commercially in The Netherlands. Each plant, which is like a small leek without a pronounced pseudostem, forms a cluster of near-spherical, white-skinned bulbs which are summer dormant. The plants are winter hardy

and, although they are normally propagated from small bulbs, they can flower and produce fertile seed and can be crossed with leeks (van der Meer and Hanelt, 1990).

Leek cultivars

Early leek cultivars were landraces that were variable in agronomic and morphological traits. Leek growers produced their own seed from selected superior plants. The varieties were often named by their locality of origin – for example, cv. 'Musselburgh' from the town of that name in Scotland. Winter hardiness was selected in northern parts of Europe and early, fast-growing landraces developed in southern Europe (de Clercq and van Bockstaele, 2002). Leek varieties have been classified into a number of major types that differ in pseudostem length and slenderness, leaf colour, winter hardiness and tendency for bulbiness (Brittain, 1988). The types are:

1. Bulgaarse Reuzen (Bulgarian Giant). Very long, high-yielding leeks, pale-green leaves, little frost resistance, e.g. cv. 'Longa'.
2. Danish types. Long, high-yielding types with pale to mid-green leaves, suitable for late summer production, rather frost susceptible, e.g. cv. 'King Richard'.
3. Franse Zomer selections. Long leeks with mid-green leaves, limited frost resistance, tendency to be bulby, e.g. cv. 'Pancho'.
4. Swiss Giant group. Medium to long, pale to mid-green, rather spreading leaves, some frost resistance; some cvs have done well as early-season modular transplants, e.g. cv. 'Tilina'.
5. Blauwgroene Herfst. Medium shank length, dark-green leaves, tendency for bulbiness in some, e.g. cv. 'Verina'.
6. Autumn Giant group. Medium shank length, mid-green, spreading leaves, little bulbing, high yields, e.g. cv. 'Goliath'; some varieties are very frost hardy.
7. Winter Giant group. Rather variable in appearance between varieties, but all have good frost resistance, e.g. cv. 'Winterreuzen'.
8. Blue-green Winter group. Short leeks, dark leaves, a high degree of bulbiness, very hardy but rather low yielding, e.g. cv. 'Bleustar'.

Types 4, 6, 7 and 8 correspond to already registered 'cultons' or cultivar groups. A culton is a systematic group of cultivated plants based on one or more user criteria (Hetterscheid *et al.*, 1999).

Rakkyo, *Allium chinense* G.Don

Allium chinense, which has also been called *A. bakeri* Regel, known as rakkyo or scallions, is grown mainly in Japan and China to produce small, edible bulbs which are mostly used in pickles in Japan. In China it is mainly grown in central and southern regions and its wild type is reported to grow in the mountain regions of Chiangsu and Chechiang provinces. The cultivated types are propagated by bulb division, since the flowers do not set seed. The chromosome

number is 32 and the plants are thought to be autotetraploids (Toyama and Wakamiya, 1990). In growth the plants resemble chives, but the leaves and flower stalks are distinctive (see Fig. 1.1).

The leaves are slender and 30–60 cm long. The crop develops rather elongated bulbs in the spring and early summer and then becomes summer dormant, the foliage withering and dying back from mid-summer until the autumn. It is therefore grown as an autumn-planted crop to produce an early summer bulb harvest. The bulbs are grey-white or purple, have a thin transparent skin and are rather oval in shape. Inflorescences, bearing an umbel of six to 30 reddish-purple flowers on a stalk 40–60 cm long, may develop in the autumn, after summer dormancy. If an inflorescence forms, the swollen leaf bases of the shoot axis where it terminates wither, and further shoot and bulb development occurs to the side of the inflorescence stalk. As a consequence, unlike the other allium crops, the inflorescence is to the side of the main growing shoot, not emerging from its centre.

There are many local strains of rakkyo in China and Japan, most of them not fully characterized, but within Japan the three cultivars 'Tama Rakkyo' (meaning ball-type rakkyo), 'Rakuda' and 'Yatsufusa' are distinct (Toyama and Wakamiya, 1990). Cv. 'Tama Rakkyo' has short, thin leaves and each plant produces ten to 25 small (1.5–3.0 g), white bulbs that are suitable for high-quality pickles. Cv. 'Rakuda' forms taller, more robust plants which typically produce six to nine rather elongated bulbs weighing 4–10 g. Cv. 'Yatsufusa' produces smaller bulbs with a narrow, firm neck and are favoured for pickling. It matures earlier and is lower yielding than cv. 'Rakuda'.

Chives, *Allium schoenoprasum* L.

This is the most widely distributed allium species. It grows wild in Eurasia and America and, being very cold hardy during its winter dormancy, it grows in arctic regions at latitudes as high as 70°N. At low latitudes it grows in mountainous areas – for example, in northern India. It is a plant of moist soils in damp meadows. Chives have been grown for their green, onion-flavoured leaves as a crop in Europe since the 16th century (Poulsen, 1990). In the wild, many ecotypes and biotypes differing in size exist, but these have been shown to be interfertile, and therefore all of the same species. The wild species is also very variable in its chromosome number. Diploids, with 16 chromosomes and tetraploids, with 32 occur, as do irregular chromosome numbers that are not multiples of 8.

The plants form dense clumps of low-growing, narrow, hollow leaves (see Plate 1, Fig. 1.1 and Table 1.2). An axillary bud develops and forms a side shoot after every two or three leaves has formed, and thereby the plants develop into a cluster of shoots. The shoots remain attached to each other on a short rhizome, and the plants do not produce bulbs. The plants become dormant in short day-lengths (see Chapter 4).

The plants are propagated vegetatively or from seed, the latter being more important for the commercial crop. Most seed is produced by open pollination of selected plants. The utilization of male sterility has enabled large-leaved F_1 hybrids to be bred, which are high yielding as 'forced' winter greenhouse crops in Germany.

Chinese chives, *Allium tuberosum* Rottl.

Allium tuberosum grows wild over much of eastern Asia, from Mongolia in the north to the Philippines in the south, and from Japan to Thailand east–west. It is a plant that easily naturalizes from cultivation, so its initial centre of origin is unclear. Chinese chives have been cultivated for more than 3000 years in China (Debin *et al.*, 2005). The plant is cultivated for its edible, garlic-flavoured leaves, young inflorescences and, in some varieties, fleshy roots. In China the shoots are often harvested after being blanched by excluding light. During dormancy it stores its reserves in rhizomes that are covered in a brown, fibrous coating formed from the remains of old foliage leaf bases. The leaves, which arise as dense clumps from the rhizome, are flat, grass-like and keeled and the scape is solid and sharp-angled (see Fig. 1.1), bearing a flat-topped umbel of white, open, star-shaped, fragrant flowers (see Plate 1). The plant is often grown as a decorative for its attractive inflorescence. It can be propagated both vegetatively and from seed, which is formed in abundance.

French grey shallot, *Allium oschaninii*

In southern and eastern France, and also in Argentina, the grey shallot cultivar 'Grise de la Drome' is cultivated for its esteemed bulbs of unique flavour (Messiaen *et al.*, 1993). The bulbs are covered with several skins that adhere together to form a grey-coloured 'shell'. The leaves are light green and the roots are thick and do not die back during bulbing. Molecular and chromosome techniques (RAPD and GISH) have shown that the grey shallot is a domesticate of *A. oschaninii*. Most of the chromosomes are from *A. oschaninii* and 1.5 chromosomes are derived from either *A. cepa* or *A. vavilovii* (Friesen and Klaas, 1998). These studies showed that *A. oschaninii*, which is in *Allium* subgenus *Cepa* section *Cepa*, is a sister group to the *A. cepa*/*A. vavilovii* evolutionary line. *Allium oschaninii* occurs in the wild in central to south-western Asia, and and its large bulbs are collected for food by local inhabitants. A homogeneous strain from 'Grise de la Drome' has been selected, subjected to meristem tip culture to remove viruses and propagated in insect-proof houses and released as improved selection 'Giselle' by the Institut National de la Recherche Agronomique (INRA), France (Rabinowitch and Kamenetsky, 2002).

Cultivated hybrids of *Allium cepa*

A number of onion types are hybrids between *A. cepa* and *A. fistulosum*, including the 'top onion' (also termed 'tree onion', 'Egyptian onion' or 'Catawissa onion'), which produces small bulbs (termed 'bulbils' or 'top-sets') instead of flowers on the inflorescence (see Fig. 4.41). These have been termed *Allium* × *proliferum* (Fritsch and Friesen, 2002). The bulbils sometimes sprout on the inflorescence, and both dormant and sprouting inflorescence shoots may be eaten and are also used to propagate the plant. Top onions are a home garden crop that used to be popular for early spring green onion production in the USA (Jones and Mann, 1963). They are also grown as home garden crops in Europe and north-eastern Asia (Fritsch and Friesen, 2002). They are seed sterile, and molecular methods have confirmed their hybrid parentage (Klaas and Friesen, 2002).

The Wakegi onion (*Allium* × *wakegi*) is a diploid hybrid (chromosome number 16) between *A. fistulosum* and a shallot-type *A. cepa*. It has been grown for centuries in Japan and China as a green salad onion crop (Inden and Asahira, 1990). It produces slender leaves 60–70 cm long and it divides freely to form many side shoots (tillers). Unlike true *A. fistulosum*, it forms bulbs in long day-lengths and it becomes dormant in summer. It is not very cold hardy and is grown in the warmer regions of Japan. Molecular and chromosomal studies have confirmed the hybrid parentage. The DNA of the chloroplasts from Japanese material hybridized with *A. fistulosum* complementary DNA, indicating that the cytoplasm derived from Japanese bunching onion, and therefore this species was the maternal parent. However, in different lines from Indonesia, analysis of chloroplast DNA indicated that both shallot and bunching onion were maternal parents, indicating multiple origins for this type of hybrid.

Hybridization between a common onion type and *A. fistulosum* gave rise to the variety 'Beltsville Bunching', which is grown as a green bunching onion, and which has the resistance to pink root disease characteristic of *A. fistulosum*. Hybrids involving shallots and *A. fistulosum* have produced the non-bulbing 'Louisiana Evergreen' and the bulbing, shallot-like 'Delta Giant', both of which are pink root resistant (see Chapter 5).

A more slender hybrid species (*Allium* × *cornutum*) – known as 'Pran' in Kashmir and shown to be identical with the Croatian cultivar 'Ljutica' – is a triploid in which *A. cepa* is the donor of two sets of chromosomes, but the origin of the third set remains unclear. It is quite widely distributed as a garden crop in Tibet, Jammu, Europe and Canada (Fritsch and Friesen, 2002).

Edible alliums of lesser or local importance

Many wild species of alliums are used by local inhabitants, particularly in the republics of central Asia, western China and southern Siberia, and the list of such

species that are well documented for the outside world continues to expand (Fritsch and Friesen, 2002). Domestication of wild plants is still continuing; for example, in the Tien Shan mountains of Kyrgyzstan, Uzbekistan and Kazakhstan, local residents sometimes transplant the large-bulbed and pungent endangered species *A. pskemense* to their gardens. The demand for novel and 'gourmet' products can drive the selection and development of new crops from wild or backyard cultivated species, for example, the cultivation of *A. ursinum* is being investigated in Switzerland. In addition, formerly cultivated types may cease to be cultivated or shrink in importance, e.g. the pearl onion type of *A. ampeloprasum* in Europe. Table 1.3 lists the allium species reported to be cultivated or collected in localized parts of the world.

ECONOMIC IMPORTANCE

Edible alliums are important crops worldwide. Based on FAO statistics for mean production, and using mean export prices as a measure of the relative values of different crops, averaged over the years 2002–2004 the value of world edible allium production was about 21% of world tomato production, 54% of world brassica production and 120% of world barley production (FAO, 2007). As regards international trade, edible alliums account for about 49% of the value of tomatoes, 186% that of cabbages plus cauliflowers and 66% that of barley as an average over the years 2002–2004. About 46% of the value of international trade in alliums is for dry bulb onions, 31% for garlic, 13% for green onions and shallots and 10% for leeks and others. The average value of international trade in alliums for the years 2002–2004 was US$2167 million, and the total weight of alliums traded was 6.7 million t. The weight of alliums in international trade represents only about 9% of total production. Averaged over the years 2002–2004, world productions in millions of tonnes were 54.2 for dry bulb onions, 13.4 for garlic and 4.4 for green onions plus shallots and, averaged for the years 2003–2005, 1.78 for leeks and others (FAO, 2007).

World dry bulb onion production increased 2.34 times between 1978 and 2002, whereas population increased 1.45 times. The area under cultivation increased by a factor of 1.9 to 2.95 million ha in this interval, and world average yields increased from 14.04 to17.4 t/ha. Onion export prices increased only from US$191 to 226/t between 1977 and the 2002–2004 mean price, a fall in real terms if inflation is accounted for. The changes for garlic are more dramatic – production increased steadily by a factor of 3.08 between 1978 and 2002. The area under cultivation increased by 1.92 times to 1.12 million ha and world average yields increased 1.6 times to 11.2 t/ha. Export prices were US$794/t in 1977, and US$465/t as the 2002–2004 mean.

Bulb onions are produced from the subarctic regions of northern Finland to the humid tropics, although they are best adapted to production in subtropical and temperate areas. Many populous, developed countries – e.g. Germany, the

Table 1.3. Allium species collected or cultivated for food in localized regions (minor crops).

Species name	Region(s) where used	English name
A. altaicum[a]	Southern Siberia	Altai onion
A. canadense[a]	Cuba	Canada onion
A. consanguinum[a]	North-eastern India	
A. glaucum[b]	Western Siberia	
A. hookeri[a]	Bhutan, Yunnan, north-western Thailand	
A. kunthii[a]	Mexico	
A. macrostemon[a]	China, Korea, Japan	Chinese or Japanese garlic
A. neapoltanum[a]	Central Mexico	Naples garlic
A. nutans[a,c]	Western and southern Siberia, Russia, Ukraine, Xinjiang	
A. obliquum	Western Siberia, Eastern Europe	Oblique onion
A. platyspathum[c]	Xinjiang	
A. psekemense	Uzbekistan, Kyrgyzstan, Kazakhstan	
A. ramosum[a,b] wild types of *A. tuberosum* (see Table 1.1)	China, western Siberia	Chinese chive or leek
A. rotundum[a]	Turkey	
A. senescens[b,c]	Western Siberia, Xinjiang	
A. ursinum[a]	Central and northern Europe	Ramsons
A. victorialis[a]	Caucasus, Japan, Korea, Europe (formerly)	Long-root onion or garlic
A. wallichii[a]	Eastern Tibet	

[a]From Fritsch and Friesen (2002).
[b]From Cheryomushkina (2005).
[c]From Jie *et al.* (2005).

UK and Japan, oil-exporting Middle Eastern countries – e.g. Saudi Arabia – and countries in the humid tropics – e.g. Malaysia, Sri Lanka and Côte d'Ivoire – are large net importers of dry bulb onions and garlic. Important dry bulb onion exporters include India, Argentina, The Netherlands, Spain, Mexico, Turkey, the USA, Poland, Australia, New Zealand and Chile. India is the world's largest exporter and supplies pungent bulbs to the Arabian Gulf states and many humid tropical countries. The Netherlands produces large quantities of long-storing, spring-sown, pungent onions, which are exported between September and April, mainly to Germany and the UK. The Netherlands also acts as a marketing intermediary, both importing and re-exporting onions. Bulbs from the southern hemisphere, notably Chile, Australia (especially Tasmania) and New Zealand have an important export market in northern Europe from May to July, when the previous year's crop in that region has reached the end of its storage life.

Within a large country like the USA the market can be supplied year-round with onions from different climatic zones. Thus autumn-sown crops grown in the southern and south-western states of Texas, New Mexico, Arizona and California produce bulbs for sale between late February and June. Crops from the irrigated mineral soils of the western states of California, Colorado, Oregon and Idaho produce large, sweet bulbs for sale from summer until January. The north-eastern and northern states of New York across to Minnesota produce pungent, long-storing bulbs for marketing between September and April.

Because of the global trade in dry bulb onions, and because of the many techniques for growing and storing onions for sale year-round described later in this book, bulb onions are available throughout the year in most countries.

Onion prices fluctuate from year to year and, because there is a global market in onion bulbs, there is little that producers in any one region can do to control the market and stabilize prices. Better communication about the areas planted in production zones, the effects of weather in real time and the state of markets worldwide are beginning to evolve. Commercial web sites that supply price information on an international basis are also starting to appear. Nevertheless, swings in supply and demand from year to year and unforeseen gluts on international markets are likely to remain part of the onion supply picture (Bosch-Serra and Currah, 2002). In Europe, the onions that are marketed must meet certain statutory quality standards (Commission of the European Communities, 1983, 1997).

Trends in global onion production are difficult to predict and depend on a complex mixture of technological and economic factors. For example, continual improvements in growing, harvesting and storage techniques, usually based on research, along with the introduction of more mechanization, have reduced the labour input and improved the quality and economics of the crop in the UK (MAFF/ADAS, 1982). As a result, national production rose eightfold between 1960 and 1981. In 1963 Egypt was the world's leading exporter of bulb onions, sending 190 million t overseas, mainly to northern Europe. Bulb onions were second only to cotton in value as an export crop. Changes resulting from Nile flood control resulted in an epidemic of white rot disease (see Chapter 5) and, in 1986, Egyptian onion exports were down to 21 million t, though they have since recovered. Thus, unforeseen consequences of technological change almost destroyed the export industry in the country with the oldest records of onion cultivation.

Shallots are of much less economic importance than their larger-bulbed relatives. They are mainly produced by small-scale and home-garden growers, but they are particularly important in the humid tropics since the local strains have the pest and disease resistance necessary to grow in that environment (Currah and Proctor, 1990). In France, they are an important commercial crop with about 2400 ha under cultivation, giving an annual production of about 50,000 t (FAO, 2007).

Garlic is the second most important allium crop. It is a component of most of the world's cuisines and, at least in the developed world, its popularity has been boosted by growing awareness of its health benefits (see Chapter 8). Climatically, regions with a reasonably mild winter with some rainfall followed by a sunny, dry summer – which is good for ripening and harvesting the bulbs – are ideal for garlic production. California has such a climate, and most of the US garlic production is there.

World production, at about 12.6 million t/year, has increased more than threefold since the late 1970s, largely as a result of a huge increase in production by China, from 2,412,477 t in 1978 to 8,153,409 t in 2001, according to the 3-year moving averages of FAO (2007) statistics. A massive increase in Chinese garlic exports over the same period, from 11,283 t in 1978 to 1,115,890 t in 2005 (FAO, 2007), has led to the current predominance of China in the world garlic trade. The high quality and low price of Chinese garlic is making it difficult for producers to compete in higher-cost regions like California, and areas planted there are declining. Import tariffs were imposed by the USA in an effort to protect the local garlic industry and the EU has quotas for imports, negotiated primarily with China and with Argentina.

There has been a tendency for local production to decline and be replaced by imports in a number of developed countries in the last decade or more, e.g. in Japan, France and Italy. Argentina is the second most important exporter of garlic, with exports fluctuating around 80,000–90,000 t in the years 2001–2005 following a steady increase in the 20 years up to the late 1990s. Spain exported around 60,000–70,000 t in 2001–2005, having increased steadily from initially small quantities since the early 1980s. In addition to fresh consumption, the production of dried garlic for use in food manufacture and garlic extracts for use in dietary supplements and pharmaceuticals are important industries (see Chapter 8).

Leeks are an important European crop. Production by the countries of the European Community (EC), totalling about 800,000 t/year on about 30,000 ha, represents only about 25% of the annual production for bulb onions. However, because the price per unit weight of leeks is about 2.7 times higher than for onions, the monetary value of the crop within the EC is about two-thirds that of bulb onions. France is the largest EC producer, with 6420 ha in 2005. Other important producers are Belgium, The Netherlands, Germany, Spain, the UK and Greece. The average yield in the major producing countries varies from 20 to 40 t/ha, with Belgium having average yields well above the EC mean (FAO, 2007). A close relative of leek, the kurrat is an important crop grown for fresh green leaves in eastern Mediterranean countries, particularly Egypt (van der Meer and Hanelt, 1990).

Japanese bunching onions, rakkyo and Chinese chives are crops of commercial importance in eastern Asia, notably Japan, Korea and China. The annual production of Japanese bunching onion in Japan is about 600,000 t, roughly half the nation's bulb onion production. However, the prices obtained

per unit weight of bunching onion are more than double those for bulb onions, so the value of the two crops in Japan is similar (Rabinowitch and Brewster, 1990a). South Korea produces about 430,000 t of Japanese bunching onions annually. China produced 16,010,000 t of bunching onion in 2001 on 478,000 ha, an increase from 3,474,600 t on 114,200 ha in 1990, a period over which total vegetable production in China approximately doubled (Debin *et al.*, 2005). Annual Japanese production of rakkyo is about 30,000 t, much being used to produce high-value pickles, and annual Chinese chive production is about 66,000 t. These latter two crops sell for a price per unit weight roughly three times that of onion bulbs in Japan, so again the relative economic importance of the crops needs to be adjusted for price differences. In China, Chinese chive production was 7,574,600 t from 232,800 ha in cultivation in 2001, an increase from 3,474,600 t from 90,000 ha in 1990 (Debin *et al.*, 2005). Exports from China of cooled fresh green alliums and pickled alliums have been increasing in recent years and were worth US$36 and 115 million, respectively in 2001 (Debin *et al.*, 2005).

Chives are widely grown as a home garden plant for use as a flavouring herb. The total world area of commercial production is about 1000 ha, with large areas in Denmark, New Zealand and Germany (Poulsen, 1990). They are grown in greenhouses in Germany following a 'forcing' treatment (see Chapter 4) to provide winter leaves.

2

The Structure of Edible Alliums

The allium crops all have a similar basic structure and in this chapter the external appearance of the crops at each stage of growth is described. The internal organization of first the vegetative and later the flowering stages is then explained. Information on the anatomy and morphology of the allium vegetables was reviewed by de Mason (1990).

VISIBLE GROWTH STAGES

When grown from seed, the allium crops go through vegetative and flowering stages of similar general appearance, although bulbing does not occur in some. Some obvious differences in leaf and flower structure have already been described in Fig. 1.2 and Table 1.2. The various stages of development of an onion grown from seed are illustrated in Fig. 2.1. Figure 2.2 graphs leaf and bulb development in a typical spring-sown crop. The earliest stages of development from seed are distinguished using the terms loop, crook, and first and second leaf stages (see Fig. 2.1B–D). The tolerance of onions to herbicides changes rapidly during these early stages, and applications must be timed accordingly (see Fig. 5.5). Garlic, shallot and rakkyo are propagated from bulbs. The first leaf to sprout from the bulb and penetrate to the soil surface is bladeless (see Fig. 2.3B). From within this, normal bladed leaves emerge to give plants similar in appearance to those in Fig. 2.1E.

OUTLINE OF THE OVERALL PLANT STRUCTURE

Figure 2.4 is a diagrammatic representation of a vegetative onion plant. The other crops have the same basic pattern of apical growth, root growth and stem development. The stem, which is below soil level, is flattened to form a disc at the base of the plant. At the top centre of the stem disc is the shoot apex, from

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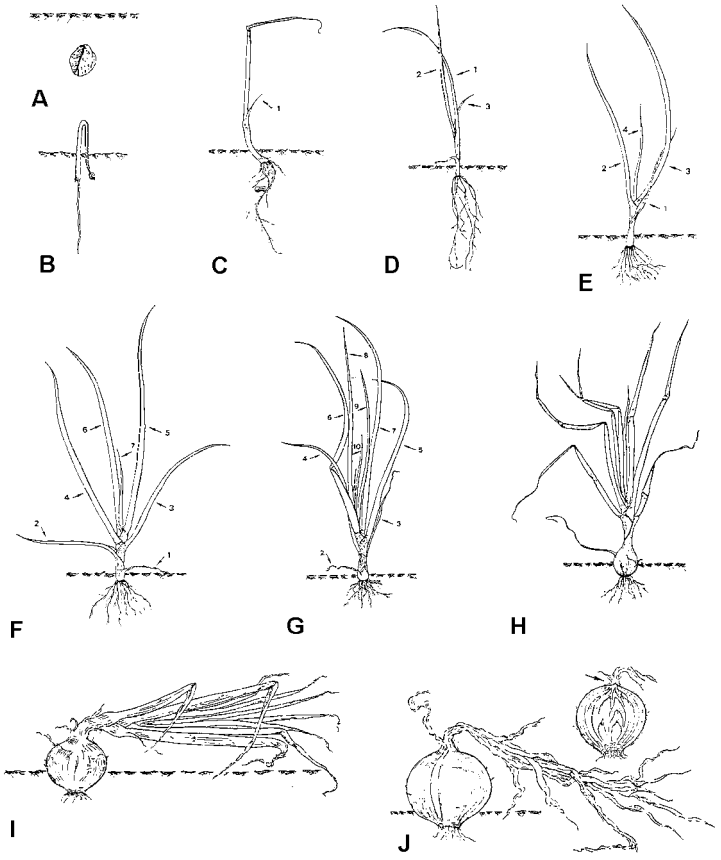

Fig. 2.1. Key stages in the growth of bulb onions from seed (from Rey *et al.*, 1974. Reproduced by courtesy of *Revue Suisse de Viticulture, Arboriculture et Horticulture*). (a) Seed in soil after sowing. (b) The 'loop' stage. After germination underground the cotyledon appears as a loop or hook above the surface. (c) First leaf 'crook' or 'whip' stage. The first true leaf appears while the cotyledon is still sharply bent to form a shape like a shepherd's crook or a whip. (d) Cotyledon senescence. After the appearance of the second and third true leaves the cotyledon desiccates, withers and falls. (e) Fourth leaf 'leek' stage. The fourth leaf appears and the neck of the plant starts to thicken while the first leaf shrivels. (f) Fall of the first leaf. The first leaf falls and the second leaf becomes detached at the sheath and begins to senesce from the tip while leaves five, six and seven appear. (g) Start of bulbing. The bulb begins to form; the second and third leaves desiccate while leaves eight to 13 appear; the plant reaches maximum height. (h) Bulb swelling. The bulb swells rapidly alongside the progressive desiccation of leaves four to six plus tips of the younger leaves. The leaves may bend or fold sharply under their own weight. One or two more short leaf blades may appear. The dry outer bulb skin begins to form. (i) 'Fall-down' or 'soft-neck'. The neck or pseudostem becomes hollow as new leaf blades cease to grow within it, and the neck tissues lose turgidity and soften so that the foliage collapses under its own weight. The bulb reaches its final size. (j) Bulb ripening. The outer skins dry, cure and set whilst the foliage senesces completely and desiccates.

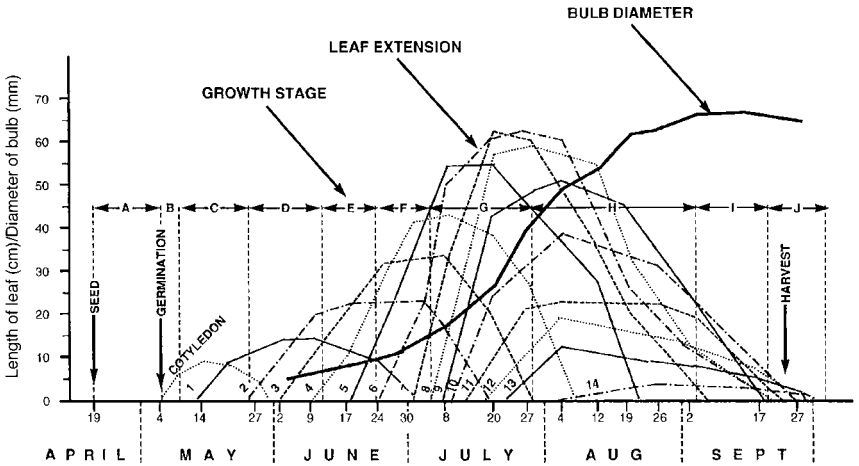

Fig. 2.2. The growth in length of successive leaves and in bulb diameter after onions were sown in mid-April in Switzerland. The timing of each growth stage in Fig. 2.1 is indicated (redrawn from Rey *et al.*, 1974).

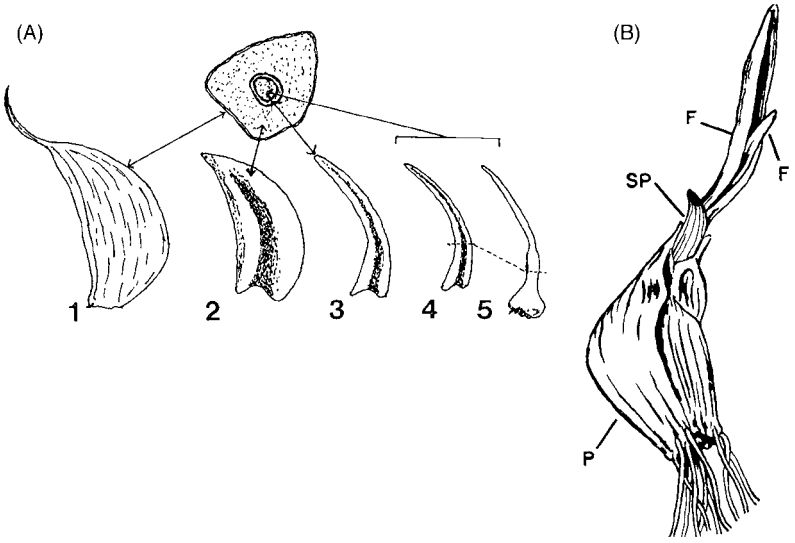

Fig. 2.3. (a) A cross-section of a single garlic clove with the corresponding parts shown below in longitudinal section as follows: 1, protective leaf; 2, storage leaf; 3, sprout leaf (bladeless); 4, first foliage leaf; 5, second foliage leaf surrounding still smaller foliage leaves, all attached to the stem. The dotted line indicates the lower limit of the leaf blade. (b) A sprouting garlic clove still surrounded by the protective leaf, P. From the clove tip protrude the sprout leaf, SP and the elongating blades of the foliage leaves, F (from Mann, 1952. Courtesy of *Hilgardia*).

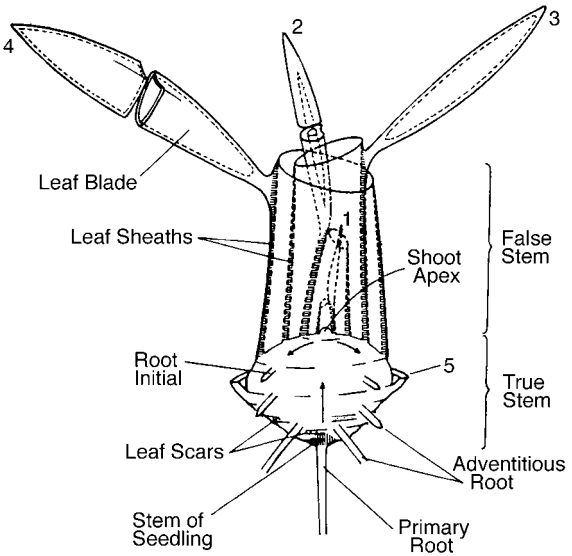

Fig. 2.4. A diagrammatic representation of the development of the stem, leaves and roots in a young onion plant. Leaf 1 is the youngest and 4 the oldest shown. As the stem grows it broadens, as shown by the divergent arrows below the shoot apex. New roots continually arise in the upper part of the stem. In this figure the space between adjacent leaf sheaths is much exaggerated (from Jones and Mann, 1963, Fig. 5. Courtesy of John Wiley & Sons Inc., New York).

which leaves are initiated oppositely and alternately, so that the leaves emerge in two ranks at 180 degrees to each other (see Fig. 2.1F). Each leaf consists of blade and a sheath. The sheath develops to completely encircle the growing point, and ultimately forms a tube that encloses younger leaves and the shoot apex. What at first sight is the stem of the plant is in fact a 'false' or 'pseudo' stem formed from concentric leaf sheaths and young leaf blades growing up the centre of the older encircling sheaths (see Fig. 2.4). At the junction of the blade and sheath there is an opening or pore where the tip of the blade of the next youngermost leaf can be seen. Ultimately, the blade of the younger leaf will elongate and emerge through this pore. On a fully elongated leaf the pore is visible at the top of the pseudostem, with younger green blades elongating through it. As new leaves are initiated and expand near the shoot apex, older sheath bases get pushed further away from the apex by continuing lateral expansion of the disc-like stem (see Fig. 2.5).

Roots are initiated in the stem near the base of young leaves and push downwards through the outer layers of the stem disc to emerge (see Fig. 2.5). The exception is the primary root, which emerges from the seed, but this normally lives only a few weeks. As the stem disc expands, the bases of older

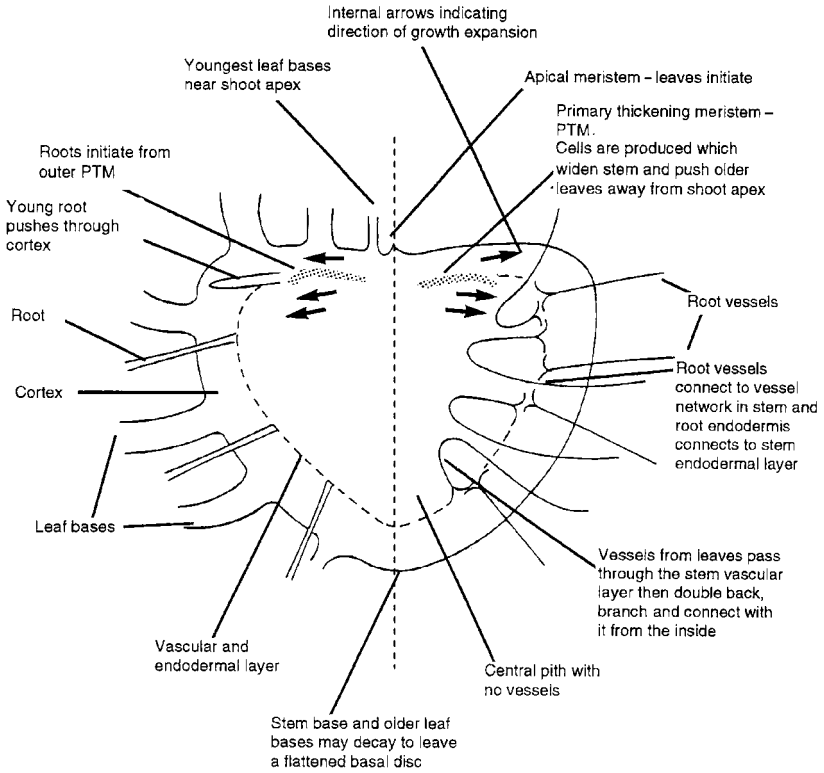

Fig. 2.5. Diagrammatic longitudinal section through an onion or garlic stem (baseplate) showing the main tissues, leaf bases, root origination and regions of cell division (left side); and how the vessels of the stem, root and leaves interconnect (right side) (based on Mann, 1952 and de Mason, 1979).

roots get pushed progressively further away from the shoot apex while whorls of new roots continue to initiate and emerge near to the apex.

Branching, which can give rise to multiple growing points as seen in tillering shoots and doubled or multiple-centred bulbs, is fundamentally no different to axillary branching on a more typical elongated stem.

A new lateral growing point can develop in the leaf axil between the original shoot apex and the youngest leaf. The lateral develops on the same side of the parent growing point as the adjacent leaf blade. Lateral growing points proceed to initiate and develop leaves in the same way as the parent apex. On such side shoots the plane in which opposite leaves are initiated is at right angles to this plane on the parent shoot. The leaves from such shoots are initially enclosed by the sheath of the leaf in whose axil they originate. When this decays they may appear as separate side shoots.

The stem remains as a compressed disc unless flowering occurs; then the shoot apical meristem develops into an inflorescence. The stem internode between the last foliage leaf and the leaf-like spathe that surrounds the inflorescence elongates to form the inflorescence stalk (scape). Nearly always, a lateral bud develops in the axil between the scape and the last foliage leaf (see Fig. 2.6). This can continue vegetative growth after flowering has finished.

Bulbs are formed from swollen leaf sheaths. Sometimes the swollen sheaths are solely those at the base of bladed leaves, as in rakkyo. At the other extreme the storage tissues of the bulb solely comprise specially modified bladeless leaves called 'bulb scales', as in garlic. In onion the outer swollen sheaths derive from bladed leaves and the inner ones are bulb scales (see Figs 2.7 & 2.8).

Having outlined the overall plant structure, each component is now considered in more detail.

THE STRUCTURE OF THE VEGETATIVE SHOOT APEX

Figure 2.9 shows the development of an onion leaf from a crescent-shaped ridge on one side of the shoot apical meristem into a structure with a leaf blade and a short sheath that encloses younger developing leaves. The frequency of

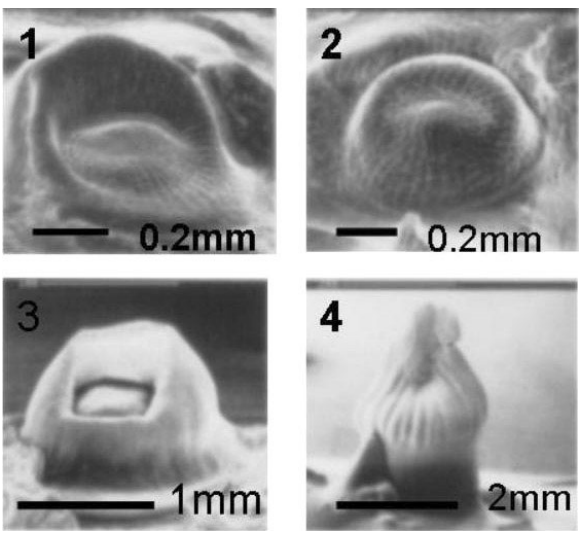

Fig. 2.6. Scanning electron micrographs of successive stages of inflorescence differentiation at the onion shoot apex. 1, non-floral; 2, early floral; 3, spathe begins to overgrow the apical dome; 4, the ridged spathe surrounds the apical dome and a definite stalk (scape) is visible. A vegetative lateral bud is adjacent to the scape, which can sometimes compete with the young inflorescence (see Fig. 4.38) (photographs courtesy of Warwick HRI, UK).

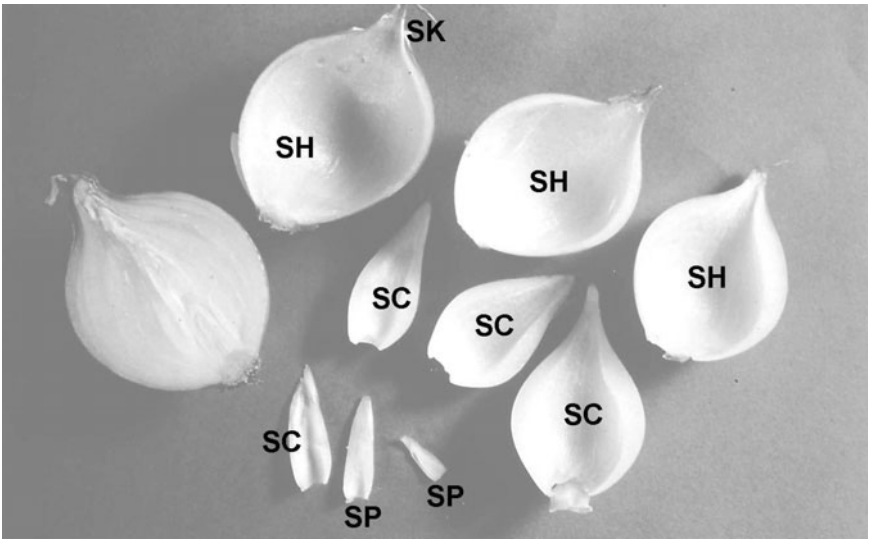

Fig. 2.7. An onion bulb dissected to show the dry outer protective skin (SK); the fleshy, swollen sheaths derived from bladed leaf bases (SH); the swollen bulb scales without leaf blades (SC); and, towards the centre, the sprout leaves (SP) with successively increasing proportions of leaf blade, which will elongate and emerge when the bulb sprouts (photograph courtesy of Warwick HRI, UK).

branching at the shoot apex varies with species, cultivar and growing conditions. For example, shoots of chives initiate a lateral every two or three leaves, thereby forming a clump of shoots (Poulsen, 1990). Onion cultivars bred to produce large, single bulbs will often produce 12 or more leaves before initiating a lateral shoot. The same is true of leeks and Japanese bunching onion, which are bred to produce large, unsplit pseudostems. On the other hand, shallots (Krontal *et al.*, 1998), multiplier onions and Japanese bunching onions grown for green shoots start to branch at lower nodes, and continue to branch more freely than the single-centred types. In onion, branching and splitting is more frequent under high temperatures and light levels.

STEM STRUCTURE

The morphology and anatomy and the development of the garlic stem (Mann, 1952) and the onion stem (de Mason, 1990) are very similar. Despite the compressed and flattened shape of the stem, some of the tissues found in a typical elongated stem can be distinguished. Figure 2.5 shows a diagrammatic longitudinal section of a stem and Fig. 2.10 a photograph of such a section from onion.

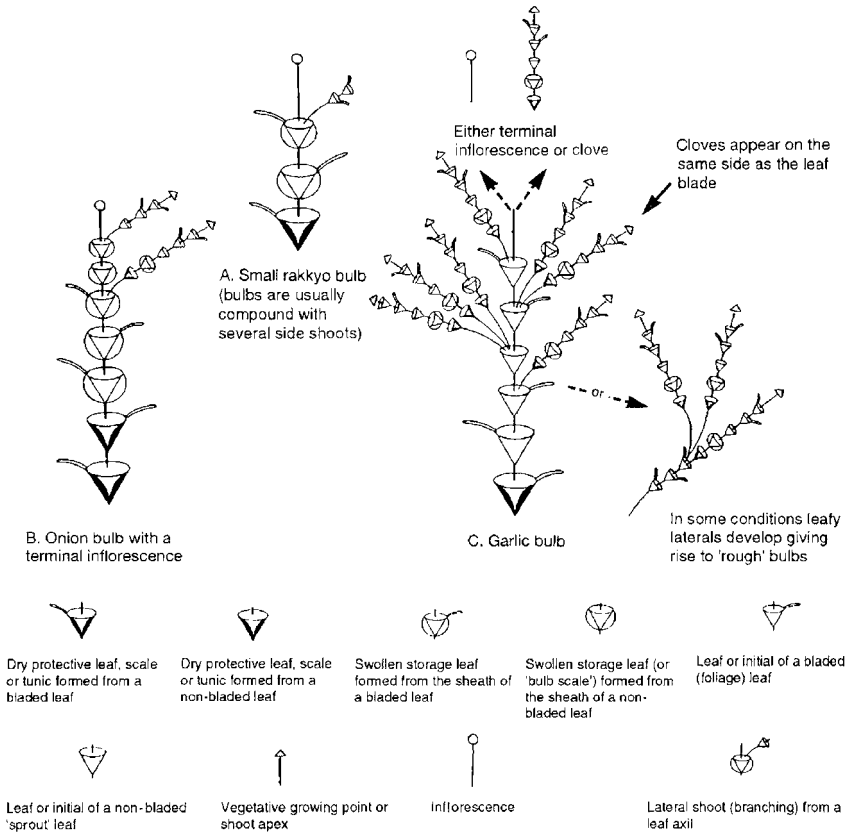

Fig. 2.8. Diagrammatic representations of the structure of edible allium bulbs of progressively increasing complexity. (a), rakkyo; (b), onion; (c), garlic.

The vessels (xylem and phloem) from the roots branch at the root base and interconnect with vessels from other roots to form a networked layer of vascular tissue that parallels the outer surface of the stem (see Fig. 2.5). Immediately external to this vascular layer is a single-celled endodermis and, external to that, a multicellular cortex. Vessels from the leaves pass perpendicularly through the vascular network formed by the root traces, but then loop backwards, divide and interconnect with the vascular network layer from its inner side. In the centre of the stem is the pith, a region devoid of vessels.

At the top of the stem, encircling the apical meristem but separate from it, is a region of cell division called the primary thickening meristem (PTM). Roots are initiated in this meristem and the cells responsible for the growth in width of the stem proliferate here. The cells of the PTM are unusual for onion in containing prominent starch granules, although these are absent during bulb dormancy (Ernst and Bufler, 1994). Young roots and their associated vascular network

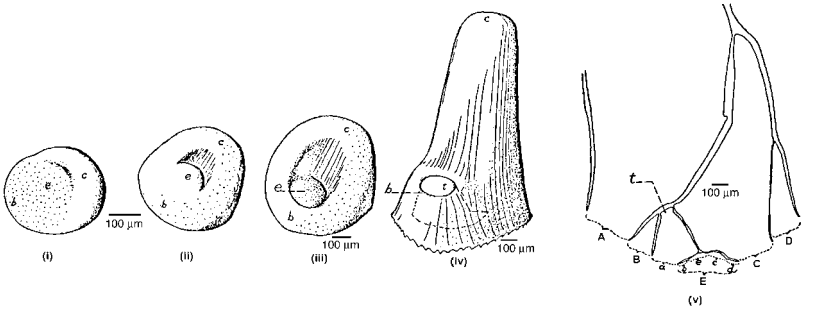

Fig. 2.9. Leaf initiation and early development at the onion shoot apex. (i) The earliest visible stage of leaf development; the new leaf appears as a crescent-shaped ridge (c) to one side of the shoot apex (e). (ii) The new leaf blade (c) begins to overgrow the apex (e). (iii) The sheath (b), as well as the blade (c), overgrow the apex (e). (iv) One side (c) has clearly formed a blade while the opposite side (b) completes the tubular sheath, with the tip (t) of a younger leaf visible through the pore at the junction of sheath and blade. (v) Transverse section of apical region. A and D, C and B and a and d are, respectively, the blade and sheath sides of successively younger leaves (from Hoffman, 1933. Courtesy of *Botanical Gazette*).

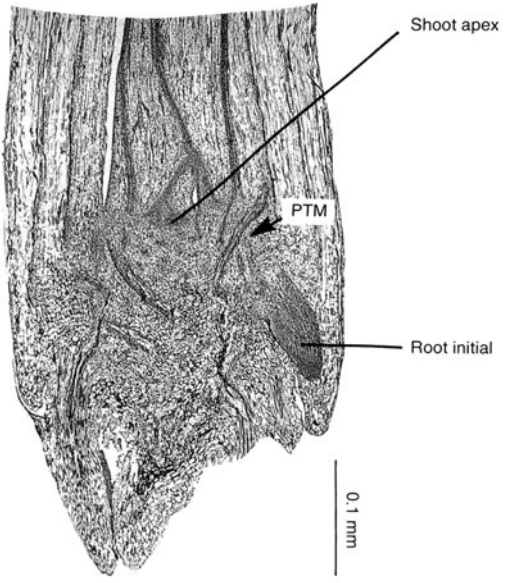

Fig. 2.10. Median longitudinal section through the stem (baseplate) of a 3-month-old onion seedling, showing a root initiating beyond the periphery of the layer of dividing cells, termed the primary thickening meristem (PTM), which causes the stem to grow in width (from de Mason, 1979. Courtesy of *Botanical Gazette*).

continuously expand and develop on the periphery of the PTM. This is paralleled by leaf initiation in the apical meristem and the subsequent expansion growth of the associated leaf bases in concentric rings away from the apex. The stem expands radially to accommodate the continuous production of roots and leaves. As this occurs, the bases of old leaves and old roots are pushed progressively further from the apex, ultimately down the side and to the bottom of the stem. After 1–2 months' growth, the thickening caused by the PTM causes the apical meristem to become somewhat sunk below the shoulders of the stem disc, resulting in a heart-shaped longitudinal section (see Fig. 2.5). Ultimately, the old leaf bases split and degenerate and are sloughed off. The underside of the stem may also start to decay, so that it becomes flattened.

The stems of the other edible allium crops are similar in general appearance to those of onion and garlic, except for Chinese chives. In this species the stem is a branched rhizome which forms a thickened, underground storage structure that connects several shoots (Jones and Mann, 1963). The rhizome is coated by a fibrous brown mat formed from the remains of decayed leaf bases. Thick, persistent roots grow from the underside of the rhizome. In Japanese bunching onion and chives, tillering results in short horizontal rhizomes connecting adjacent shoots, but the older portions die off, leaving the clusters of mostly unconnected shoots.

BULB STRUCTURE

The bulbs of rakkyo, onion and shallot and garlic show a gradation of increasing complexity (see Fig. 2.8). Bulbs in the true sense do not form in Japanese bunching onion, chives or Chinese chives, although the thickened basal sheaths may act as food reserves during winter dormancy in the former two species. In *Allium ampeloprasum*, great-headed garlic, pearl onions and most wild types form bulbs but, with leek and kurrat, bulbs form only in some specimens after bolting or in unnaturally long photoperiods (see Chapter 4).

Rakkyo bulbs form as a result of swelling of the foliage leaf sheaths, and these appear as concentric swollen rings in transverse section. There is some growth of leaf blades as the sheaths thicken, resulting in oval-shaped bulbs. The leaf blades decay at the end of bulbing. Many lateral buds form in the axils between sheaths, and these develop into the following season's shoots. The apical buds of the bulb-forming shoots differentiate into inflorescences during bulb formation and dormancy.

The early stages of bulb formation in onion and shallot are similar to those in rakkyo, involving the swelling of leaf sheaths. The thickening of the sheaths is frequently preceded by their sudden elongation. Thickening occurs as a result of lateral expansion of cells in the lower third of the sheaths and does not involve cell division. During bulbing the young developing leaves cease to form blades but develop into swollen, bladeless 'bulb scales'. In all but these leaves the length from the base of the sheath to the pore where the next leaf emerges, and which marks

the beginning of the leaf blade, is always less than the blade length. So a ratio (blade length:sheath length), termed the 'leaf ratio', of less than unity for any developing leaf is characteristic of bulbing (Heath and Hollies, 1965) (see Fig. 4.26). Bulbing can also be characterized by increases in the ratio (maximum bulb diameter:minimum pseudostem diameter), which is termed the 'bulbing ratio'. Although more easily measured than leaf ratio, initial increases in bulbing ratio depend on the extent of swelling in the sheaths of bladed leaves, and this increases with light intensity and nitrogen deficiency. Therefore, decreases in leaf ratio are a more reliable measure of bulb initiation than increases in the bulbing ratio.

As the bulb ripens, the outermost one to three sheaths develop into thin, dry protective skins. Since leaf blades cease to form on the inner bulb scales, the pseudostem becomes hollow. Also, the sheath tissues in the middle region of the neck soften and lose turgidity, ultimately causing the foliage to fall (see Fig. 2.11). This foliar fall-over is a useful indicator of bulb maturity. A typical onion

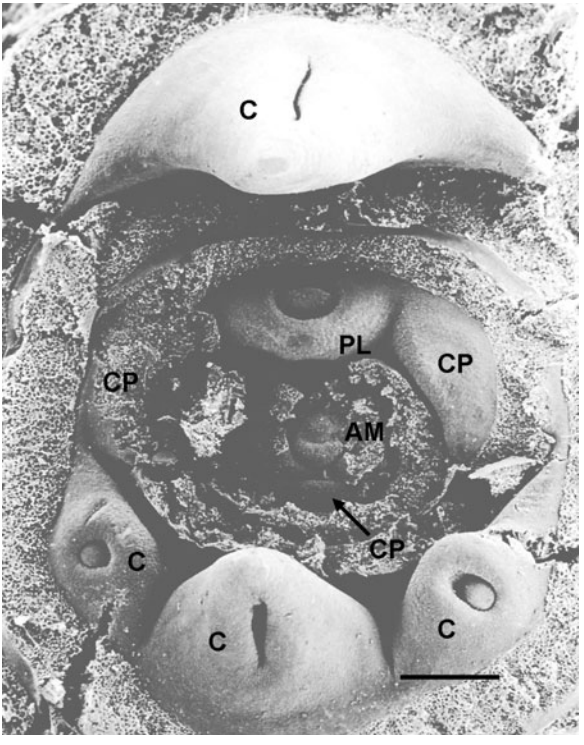

Fig. 2.11. Scanning electron micrograph of the apical region of a cold-treated garlic plant 6 weeks after planting. The leaf bases have been removed and concentric groups of cloves are differentiating in the axils between the leaf bases. C, clove; CP, clove primordium; PL, protective leaf; AM, apical meristem. The scale bar is 500 μm (0.5mm) (from Rahim and Fordham, 1988. Courtesy of *Scientia Horticulturae*).

bulb at maturity has two dry skins enclosing four swollen sheaths from bladed leaves. These in turn enclose three or four swollen, bladeless bulb scales, and finally at the centre are found five leaf initials with blades (see Fig. 2.7). These inner bladed leaf initials emerge when the bulb sprouts (see Fig. 7.5), and hence are termed the 'sprout leaves'. Usually, one or more lateral shoots occur towards the centre of the bulb, consisting of a few swollen, bladeless bulb scales enclosing several sprout leaves or, nearer the centre, just sprout leaves.

The reserve tissue in garlic bulbs consists solely of bladeless storage leaves, which constitute about 75% of the weight of trimmed bulbs and form the bulk of the familiar garlic clove. They arise as buds within the axils of the sheaths of foliage leaves, on the side of the axis below the leaf blade. Each clove primordium may divide as the axil in which it develops expands, so that up to six or seven cloves can be found in the axil of a single foliage leaf (see Fig. 2.11).

In a typical mature bulb, the number of cloves per leaf axil increases from one or two in the innermost leaf axil to six or seven in the fourth youngest axil and then decreases again in the axils of older leaves. Ultimately, the apical bud may also develop into a clove. In plants grown from very small cloves, the terminal clove may constitute the only storage leaf; such single-cloved bulbs are termed 'rounds'. The sheaths of the foliage leaves remain non-swollen, but dry to form a papery protective envelope surrounding the cloves within. When the bulb is fully ripened, the original stem and leaves are dead, and merely act as dry container for the dormant cloves. As bulbs ripen, parenchymal cells degenerate and collapse on the inner side of the leaf sheaths that form the pseudostem. This leaves alive just the outer epidermis, the conducting vessels and some surrounding cells. As a result the neck of the bulb softens and the foliage collapses, as in onion (Mann, 1952).

Individual cloves consist of a tough, outer, dry protective leaf, a swollen storage leaf that constitutes the bulk of the weight and which contains 30–40% dry matter, a sprout leaf and three or four foliage leaf primordia surrounding the apical meristem (see Fig. 2.3A). The protective, storage and sprout leaves have only vestigial leaf blades, but the foliage leaf primordia have blades. As with onion bulbs, two or so additional foliage leaf primordia differentiate at the clove apical meristem during storage. During sprouting, the sprout leaf elongates and emerges from the pore at the tip of the storage leaf, and then the first foliage leaf pushes through the pore near the tip of the sprout leaf (see Fig. 2.3B). In development, the protective leaf forms first and this ensheaths the developing storage leaf (see Fig. 2.11).

Ideally, ripe garlic bulbs should be near circular in transverse section and covered by several outer skins; such bulbs are termed 'smooth'. In some conditions (see Fig. 4.47), lateral buds may initiate in the axils of the outer leaf blades and give rise to green side shoots, which themselves go on to develop cloves, resulting in bulbs made up of several sub-clusters of cloves. Such bulbs have an irregular outer surface and are termed 'rough'. This is a common defect in garlic production (see Fig. 2.12).

Fig. 2.12. Rough and smooth garlic. Top row: bulbs planted 21 October at Davis, California from planting stock stored at 5°C for 9 weeks; all are rough. Note that the small side bulbs have separate tops, the remains of leafy axillary shoots visible in green, immature plants. Bottom row: bulbs planted 30 September from planting stock stored at 20°C for 6 weeks; most are smooth (from Mann and Minges, 1958. Courtesy of *Hilgardia*).

The bulb structure of great-headed garlic is similar to that of garlic. It frequently forms a single terminal clove or 'round'. In the following season a round usually develops an inflorescence surrounded by multiple axillary cloves, like normal garlic except that the clove size is usually larger (van der Meer and Hanelt, 1990). Frequently, additional smaller cloves or bulblets form in the outer leaf axils of the bulbs, a feature that is occasionally observed in leeks.

The structure of rakkyo, onion and garlic bulbs is diagrammatically summarized in Fig. 2.8.

FOLIAGE LEAF STRUCTURE

Studies on onion leaf anatomy have shown the tissues typical of most green leaves (de Mason, 1990). There is an outer epidermal layer coated with a waxy cuticle that contains many sunken stomata. Below this are three or four layers of columnar palisade cells. Within the palisade layer are numerous interconnecting elongated cells called laticifers. These contain the milky fluid that oozes when an onion leaf is cut across. This fluid is rich in sulfur-containing flavour compounds (Hayward, 1938). Below the palisade cells are about two layers of larger and rounder cells surrounded by much intercellular air space. Many chloroplasts occur within these cells, close to the cell walls adjacent to the air spaces. Below these chlorophyll-dense layers lie the vascular bundles surrounded by large parenchymatous cells containing fewer chloroplasts than the outer layers. The leaf cavity is lined by senescent cells lacking in protoplasm.

The vascular bundles are surrounded by a compact layer of elongated cells that form a bundle sheath. The chloroplasts in this layer of cells have been shown to contain starch (Wilson *et al.*, 1985).

In transection the garlic leaf blade shows similar tissues on both sides of the leaf (Mann, 1952), with well-defined palisade layers. The vascular bundles occur in two layers, one closer to the outer surface and the other closer to the inner (adaxial) leaf surface. The central parenchyma undergoes some cell breakdown to produce intercellular air spaces. Below the palisade layer are numerous laticifers.

During the early stages of onion foliage leaf growth, while the leaf is within the sheath of the next older leaf, the leaf blade elongates but the sheath does not. When the leaf tip emerges from the pore of the older leaf the sheath begins to elongate also (Heath and Hollies, 1965). Initially, cell division occurs throughout the length of the onion leaf blade, but it continues for longest in the basal parts, so these give rise to a large proportion of the fully grown blade. During enlargement, the cells in the central region do not keep pace with the enlargement of the outer layers, and the central cavity develops within the leaf. Later, some of the inner parenchymal cells decay, adding to the size of the cavity (Hayward, 1938).

THE ROOT SYSTEM

The roots of the allium vegetables are comparatively thick and sparsely branched as compared with those of most crop species. They lack root hairs except when they are grown in moist air rather than in soil or solution culture. Sections through onion roots show the usual series of layers from an outer epidermis, a multicellular, thick cortex and an endodermis that surrounds the central stele, which contains phloem and xylem vessels with their associated parenchymatous cells (see Fig. 2.13A; de Mason, 1990, Stasovski and Peterson, 1993).

Onions have been one of the most frequently used species in investigations of root anatomy and physiology, probably because they can be conveniently produced from bulbs and, being fairly thick, straight and unbranched they are easy to handle. Hence there is a wealth of detail available on their structure and also ultrastructure, as revealed by electron microscopy (Ma and Peterson, 2001), and how this relates to both nutrient uptake (Cholewa and Peterson, 2004) and water uptake (Barrowclough *et al.*, 2000). As the root develops, various cell layers change and mature (see Fig. 2.14).

Of particular interest is the development of the exodermis immediately below the outermost epidermal layer of cells (see Fig. 2.13). The exodermis consists of long and short cells (see Fig. 2.13C) and, somewhat later than the endodermis (see Fig. 2.14), these cells develop a water-impermeable, suberized Casparian strip in their radial walls. The long cells and some of the short cells

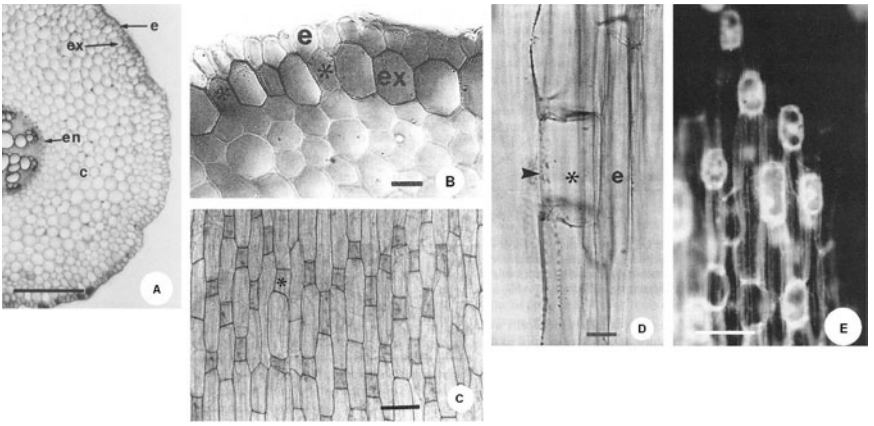

Fig. 2.13. Sections of onion roots illustrating, in particular, the structure of the exodermis with long cells that become suberized and water impermeable, and short cells that remain non-suberized and alive in older roots and even after long periods of water stress. (a) Transverse section stained with toluidine blue. Scale bar = 250 μm. c, cortical parenchyma; e, epidermis; en, endodermis; ex, exodermis. (b) Cross-section stained with Sudan red 7b, which shows up the deposition of water-impermeable suberin in cell walls: e, epidermis; ex, exodermis. The walls of the exodermal cells are positively stained except for those of a few short cells, which are indicated by asterisks. Scale bar = 25 μm. (c) A paradermal section, partially cleared and stained with trypan blue. Short cells, such as the one indicated by an asterisk, stain blue. Scale bar = 70 μm. (d) Median longtidunal section of an onion root stained with Sudan red 7b; e, epidermis. The inner tangential wall (arrowhead) of the short cell (asterisk) is unstained, indicating that it is not suberized and is therefore likely to be permeable to soil water. Scale bar = 15 μm. (e) Paradermal section of root from a plant that had not been watered for 200 days. Stained with fluorescein and viewed under blue light. There is a striking accumulation of fluorescein in the cytoplasm and nuclei of the short cells of the epidermis, which indicates that they were alive, whereas long cells are unstained and were therefore dead. Scale bar = 100 μm. (a and e from Stasovski and Peterson, 1993. Courtesy of *Canadian Journal of Botany*; b, c and d from Kamula *et al.*, 1994. Courtesy of *Plant, Cell and Environment*).

go on to develop water-repellent suberin lamellae on all their cell walls. Consequently, water and nutrient ion entry into the roots becomes restricted to those short cells lacking suberin lamellae. Hence, water and ion entry into the inner cell layers of the root involves crossing the living plasmalemma membrane bounding the cytoplasm of these cells and is subject to metabolic control there (Barrowclough. *et al.*, 2000; Cholewa and Peterson, 2004). When onion roots are subject to drought the root tips die, as do the epidermal cells external to the suberized exodermis (Stasovski and Peterson, 1993). The inner tissues remain protected from water loss by the outer suberized shell of

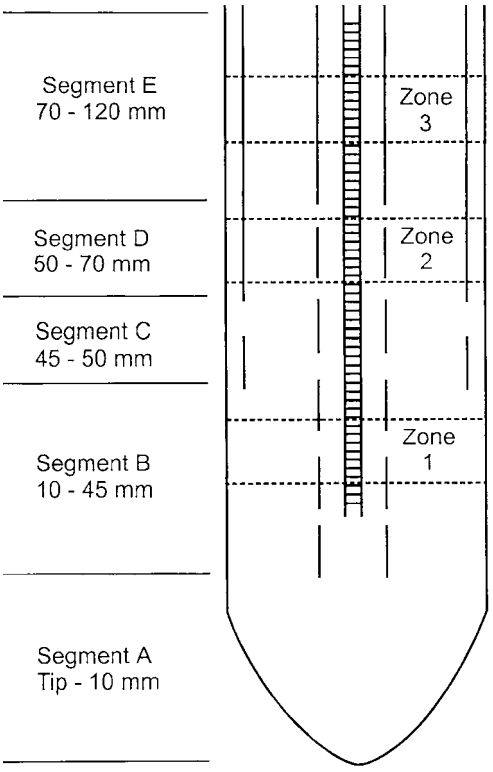

Fig. 2.14. Diagram of an onion root (not to scale) showing positions of early metaxylem (central ladder-hatched structure), Casparian bands (dashed lines), Casparian bands plus suberin lamellae (solid lines) in the endodermis (at edge of central stele) and exodermis (near root surface). Segment A, immature endodermis and exodermis; segment B, endodermis with Casparian bands, immature exodermis; segment C, developing exodermis with Casparian bands and sometimes also suberin lamellae; segment D, endodermis with Casparian bands, exodermis with Casparian bands and suberin lamellae; segment E, endodermis and exodermis with both Casparian bands and suberin lamellae. The water conductivities of Zones 1,2 and 3 were measured in experiments (from Barrowclough *et al.*, 2000. Courtesy of *Journal of Experimental Botany*).

the exodermis. These cells, along with the remaining unsuberized exodermal short cells, which expose a living plasmalemma surface representing just 0.47% of the root surface-area (Kamula *et al.*, 1994), can remain alive for up to 200 days (see Fig. 2.13E).

In addition to controlling the pathway of nutrient flow into the root cortex, there are other roles that the exodermis may play in the functioning of roots. The short cells may provide entry points for arbuscular mycorrhizae (AM) (see

Chapter 5). The AM hyphae increase the nutrient-absorbing surface of the root and may prolong its absorbing life. Also, the suberized exodermis, by preventing the death of cortical cells in drought, may provide a protected environment for AM as well as giving protection from pathogens and pests (Peterson, 1992).

Apart from very young seedlings, the bulk of the root system is made up of the adventitious roots which originate in the primary thickening meristem near the top of the stem (see Figs 2.5 and 2.10). These emerge from all sides of the stem and tend to grow near horizontally for some distance before turning downwards.

Laborious investigations of root development in onion, leek and garlic were made by Weaver and Brunner (1927). All three crops have similar root systems, and Fig. 2.15 shows the leek root system at various stages of development. The roots vary between 2.0 and 0.5 mm in thickness and are fairly sparsely branched, with one to two lateral branches per cm of primary

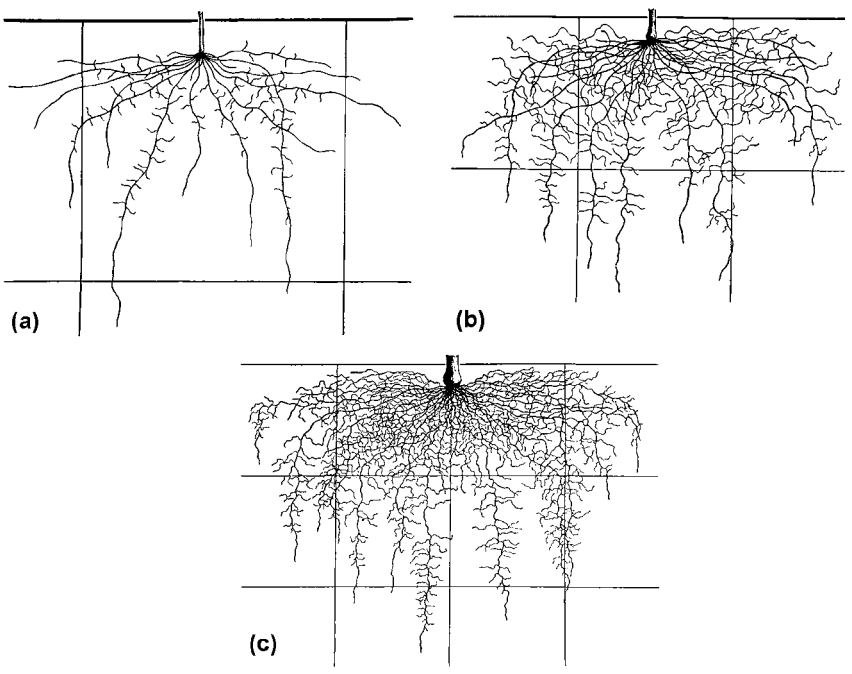

Fig. 2.15. Stages in the development of the root system of leek plants grown in rows 1 m apart with 10 cm between plants within the rows. Seeds were sown in mid-March in a well-structured loam at Norman, Oklahoma, USA: (a) roots of 2-month-old plant; (b) half of the roots of a 3-month-old plant; (c) 25% of the roots of a 4.5-month-old plant. The scale lines show a 30 cm (1 foot) square grid (from Figs 11, 12 and 13 of Weaver and Brunner, 1927).

root. Lateral branches rarely re-branch; as a result, the root length per unit volume of soil, L_V, under allium crops is low compared with that of other crop species. There are only small differences in root morphology between different onion cultivars, although older Dutch cvs had a slightly higher L_V than modern cvs (de Melo, 2003).

However, a comparison of the roots of bunching onion, *A. fistulosum*, with common onion showed that the former produced 1.29 cm of root per mg of shoot dry weight as against 0.52 cm/mg for onion. *A. fistulosum* also spread its roots further from the plant and deeper into the soil. The difference in L_V is a result of more fine lateral branches on the main roots of *A. fistulosum* (see Fig. 2.16).

The development pattern of root systems is always variable and can be influenced by both soil compaction and the distribution of nutrients in the soil. In one study the root length under an onion crop increased as the crop grew as described by the equation:

$$\log_e L = 3.4 + 1.5 \log_e W - 0.035T \qquad \text{(Eqn 2.1)}$$

where L is the total root length per unit of soil surface (km/m^2), W is the crop shoot dry weight (t/ha) and T is days from sowing (Greenwood *et al.*, 1982). Ninety per cent of the root length was found in the top 18 cm of soil throughout the season, unlike other crops that rooted more deeply as the

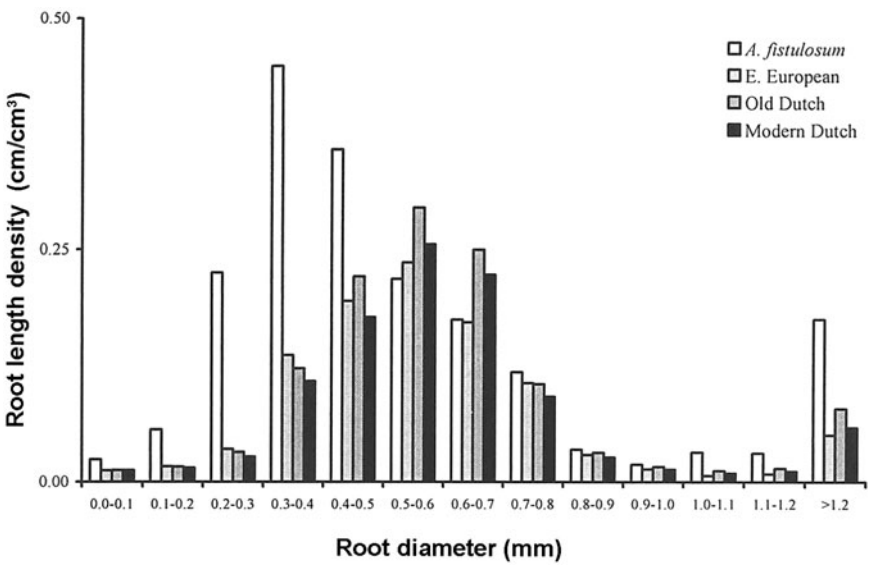

Fig. 2.16. The distribution of root length density (mean length of root per unit volume of soil (cm/cm^3) in different root diameter categories in *A. fistulosum* and in Eastern European and old and modern Dutch onion cultivars (from de Melo, 2003. Courtesy of Wageningen University, The Netherlands).

season progressed and their root weight increased. It may be that the rather sparse root system is a reflection of these crops having evolved from wild species in which mycorrhizal (VAM) enhancement of the root-absorbing surface was usual (see Chapter 5).

INFLORESCENCE AND FLOWER STRUCTURE AND DEVELOPMENT

Bolting, or inflorescence production, can occur in all the vegetable alliums and the process is similar in all. Successive stages of inflorescence initiation in onion are shown in Fig. 2.6. The inflorescence develops from the shoot apical meristem under appropriate environmental conditions (see Chapter 4). The inflorescence terminates the shoot, so further vegetative growth after flowering must occur from the lateral bud that usually develops adjacent to an inflorescence.

The internode between the last leaf and the spathe is the only stem node to elongate. In onion it ultimately forms an inflorescence stalk (termed a 'scape') that is 1–2 m long. As the scape elongates, cell division becomes confined to the more basal regions, and proceeding towards the tip the cells become progressively more elongated and mature. Consequently, elongation occurs predominantly in the lower parts of the scape. The mature onion scape is hollow, with a prominent swelling about one-third of the way from its base. It is green, covered in stomata and similar in internal anatomy to a foliage leaf (de Mason, 1990).

The other edible alliums produce similar scapes, although these differ in stature depending on the size of the plants. In rakkyo the scape is 40–60 cm long, in chives up to 70 cm long. Not all species have hollow scapes (see Fig. 1.2), and the presence or absence of swellings on the scape varies with species, Japanese bunching onion having a nearly parallel-sided scape. The scape emerges from ensheathing foliage leaves except in rakkyo, which is autumn flowering. Here, the scape emerges from the bulb after a period of summer dormancy during which the surrounding leaves wither. The foliage that elongates with the scape is from a bud in its axil, and hence the flower stalks are off-centred from the leafy shoots.

The development of individual onion flowers has been described in detail by Jones and Emsweller (1936). Underneath the spathe on the broad top of the stem numerous membranous bracts develop, each covering several young florets arising on kidney-shaped regions of dividing cells. Looking from the outside towards the centre of each floret there develop three members in each of five whorls of floral organs: the outer perianth, the inner perianth, outer stamens, inner stamens and the carpels. These develop as globose projections, with the outer whorls developing first (see Fig. 2.17a). The carpels develop as three U-shaped upswellings on the surface within the inner stamens. These upswellings grow towards the centre and their inturned edges meet, fold

within themselves and form the ovules, two of which occur in each carpel. The style arises at the apex of the three fused carpels, and is still elongating when the flower opens (see Fig. 2.17b).

The development of the inflorescence, florets and top-sets in garlic is shown in Fig. 2.18. Development to anthesis in garlic is rare and, when it can occur, requires a specific sequence of conditions (see Chapter 4). Usually top-sets (sometimes termed bulbils) form in the inflorescence and swell to suppress the florets (see Fig. 2.18E–G). The same can happen in onion, leek and other species under certain conditions (see Figs 4.35 and 4.41).

The inflorescences of these crops are umbels (see Plate 1). When ripe, the leafy spathe that encloses the umbel during development splits and the inflorescence opens. The flower colour and the pattern of opening of individual flowers within the umbel vary with species (see Table 1.2). Individual flowers are carried on short stalks (pedicels). In onion, flowers are continuously carried to the outer boundary of the inflorescence by elongation of the pedicels before the tepals open. This leads to successive cohorts of flowers opening over the whole surface of the umbel. In onion there are commonly 200 to 600 flowers per umbel, depending on cultivar, growing conditions and whether the umbel is formed from the main growing point or an axillary shoot. Similar umbels containing large numbers of flowers are produced by leeks and Japanese bunching onions. Chives typically have about 30 flowers per umbel, rakkyo six to 30 flowers and Chinese chives have approximately 40 white, star-shaped, fragrant flowers in a flat-topped umbel.

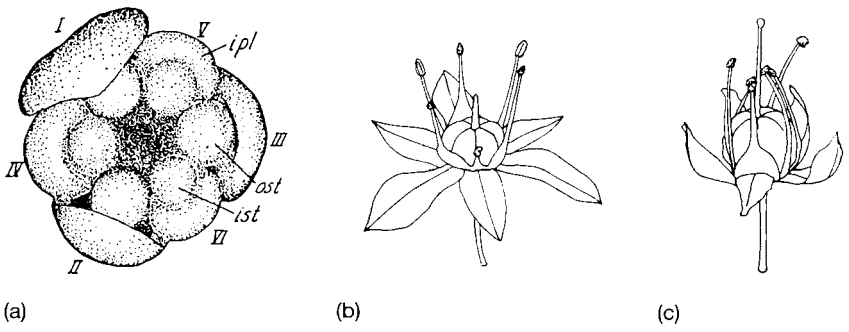

Fig. 2.17. The development of individual florets. (a) Top view of a young flower in which primordia of all perianth segments (labelled I to VI) and stamens have differentiated: ipl, inner perianth lobe; ost, outer stamen; ist, inner stamen (× 60) (from Jones and Emsweller, 1936. Courtesy of *Hilgardia*). (b) Open flower with the inner whorl of anthers shedding pollen. (c) Late in flowering when the stigma is still sticky and receptive but the tepals and anthers are withering (b and c approx. × 2) (from Currah and Ockenden, 1978. Courtesy of *New Phytologist*).

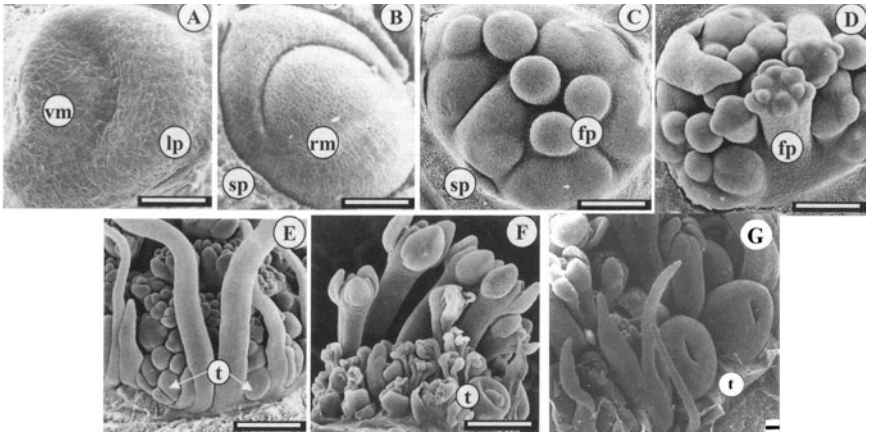

Fig. 2.18. Scanning electron photomicrographs of garlic apical and floral development. (a) Vegetative meristem (vm) with differentiated leaf primordium (lp); bar = 0.1 mm. (b) Floral transition; the reproductive meristem (rm) is swollen and hemispherical; the spathe (sp) was removed; bar = 0.1 mm. (c) Differentiation of flower primordial in a reproductive meristem with spathe removed; first flower primordia (fp) are initiated in an apex of diameter 0.8 mm; bar = 0.3 mm. (d) Differentiation within the floral primordial; floral parts are seen in the oldest floral primordial (fp) while the younger ones still appear as undifferentiated meristematic domes; bar = 0.4 mm. (e, f and g) Newly developed meristems appear near leaf-like bracts at the base of the inflorescence; they quickly differentiate and grow to form small inflorescence bulbs termed top-sets (t); bar = 0.8 mm in E, 1 mm in F and 0.1 mm in G. (a–f from Kamenetsky *et al.*, 2004. Courtesy of *Journal of the American Society for Horticultural Science*; g from Kamenetsky and Rabinowitch, 2001. Courtesy of *Sexual Plant Reproduction*.)

In each flower nectar accumulates in three cups formed between the lower ovary walls, where the nectaries are located under a small flap, and the broad bases of the filaments of the inner whorl of stamens. The stages of flower opening in onion are: (i) opening of the tepals and the beginning of nectar secretion; (ii) dehiscence and pollen release by the stamens (see Fig. 2.17b); then (iii) the stigma becomes sticky and receptive when the anthers have ceased to shed pollen (see Fig. 2.17c).

SEEDS

The development of onion seeds following fertilization is described by Rabinowitch (1990b) (see also Figs 6.17 and 6.18). Seed size and therefore the number of seeds per g varies with species; approximate figures are: onion and Japanese bunching onion, 300; leek, 350; kurrat, 440; chives, 1150. The

internal structure of the onion seed is illustrated in Fig. 2.19. The embryo is curled within the seed and consists of a short root below the shoot apex, which is located along with the primordium of the first leaf at the base of a slit at the lower end of the cotyledon. Following germination, the first leaf will emerge from this slit. The cotyledon forms the bulk of the embryo and consists mostly of small cells densely packed with reserves of globular fat, protein and sugar phosphate (phytin) (de Mason, 1990). The beginning of conducting tissue is seen as a central procambial strand. At the tip of the cotyledon, embedding into the surrounding endosperm, there is a swelling termed the haustorium. During germination this absorbs nutrients from the endosperm reserves and transfers them to the growing cotyledon. The cells of the thick-walled endosperm are also packed with reserve globules of protein and lipids.

During germination the lower portion of the cotyledon elongates first and the root emerges. Cell divisions occur throughout the cotyledon as it initially elongates. The primary root grows downwards and the slit containing the

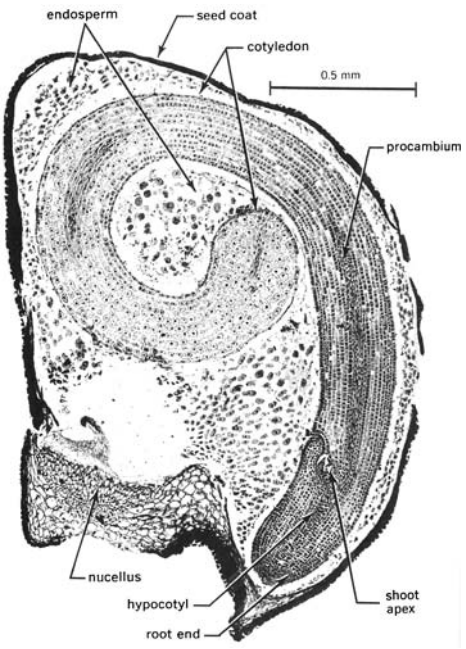

Fig. 2.19. Longitudinal section through a mature onion seed with embryo. The embryo consists of a root, a hypocotyl with shoot apex and a long cotyledon. The procambium extends the entire length of the embryo. The cotyledon ends in a haustorium, which absorbs nutrients from a thick-walled endosperm during germination. A small amount of nucellus lies under the seedcoat at one end (from Esau, 1977. Courtesy of John Wiley and Sons Inc., New York).

apical meristem remains at seed-sowing depth, while a sharp, inverted U-shaped bend develops in the cotyledon, midway between the apical slit and the haustorium, which stays embedded in the seed. The bend forms a sharp 'knee', which is pushed upwards through the soil surface by the elongation of the cotyledon on either side of it. As a result, the cotyledon emerges from the soil as a loop, before straightening and finally pulling the tip clear of the soil (see Fig. 2.1C). The same pattern of germination and emergence occurs in the other seed-grown vegetable alliums.

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3

The Genetics and Plant Breeding of Allium Crops

INTRODUCTION

The edible allium crops traditionally fall into two groups as regards the breeding and selection of new cultivars. The main group, which includes onion, leek, Japanese bunching onion and chives, consists of fertile species that produce seeds normally. The second group, which includes garlic, rakkyo, great-headed garlic and the various crops derived from crosses between *Allium cepa* and *A. fistulosum*, rarely produce fertile seeds and are reproduced vegetatively. Chinese chives produces seeds, but frequently normal meiosis does not occur and seeds are genetically identical to the mother plant; however, fertile types also exist and have been used to develop new cultivars.

The techniques of conventional plant breeding, which involve repeated cycles of hybridization between pollen donor (male) and female parent lines followed by selection and intercrossing of the offspring of such crosses, are applicable only to fertile species. The discovery and exploitation of fertile garlic has begun to change the situation for this crop, and cross-breeding and seed production are under way (Etoh and Simon, 2002; Zewdie *et al.*, 2005). Moreover, the techniques of genetic transformation and somatic cell hybridization now make it possible to transfer novel genes into the vegetatively propagated species.

Research on genetics and genomics of alliums is reviewed in several chapters of Rabinowitch and Currah (2002). The breeding and genetics of onions was reviewed by Pike (1986) and Dowker (1990). Leek breeding has been reviewed by Currah (1986), Pink (1992) and de Clercq and van Bockstaele (2002). Aspects of Japanese bunching onion breeding are summarized by Inden and Asahira (1990) and chive breeding by Poulsen (1990). Pollination biology has been reviewed by Currah (1990). These reviews give fuller references to original research reports than does the present chapter.

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THE CHROMOSOMES

Chromosome appearance and behaviour (cytogenetics) in alliums was described by Jones (1990). The basic chromosome number for this group of plants is usually eight and therefore, except in unusual cases, the number of chromosomes that can be seen during cell division is a multiple of eight (see Table 1.2). In leeks and chives one to three additional small 'supernumerary' chromosomes sometimes occur. The eight basic chromosomes in onion can be distinguished by their lengths, the ratios of the two arms either side of the centromere and dark-staining bands, and on this basis they have been numbered one to eight (see Fig 3.1; de Vries, 1990). This is important in studies that map the location in the chromosome where particular genes are located (see Genetic Linkage Maps, this chapter).

The 32 chromosomes of leek are thought to have originated as a doubling-up of an original set of 16 in an ancestral plant. Such a plant is termed an 'autotetraploid'. Because such a plant has double the diploid number of chromosomes each set of chromosomes, instead of carrying the diploid's two

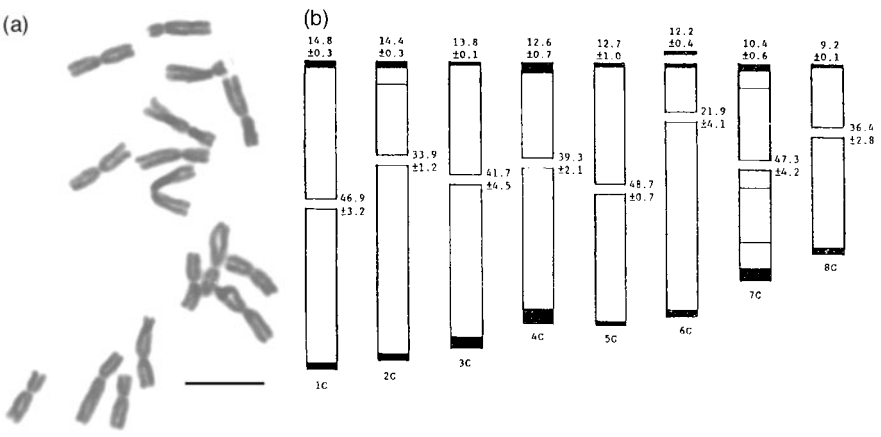


Fig. 3.1. (a) The chromosomes of shallot, *Allium cepa*, during cell division (mitosis) at the c metaphase stage, showing the 16 chromosomes each dividing into two replicates. Scale bar = 10 μm (photograph courtesy of Dr R.N. Jones). (b) Diagramatic representation of onion chromosomes numbered 1C to 8C according to the agreed naming system (de Vries *et al.*, 1990). The numbers at the top are the relative lengths; the numbers by the break in each chromosome, which represents the centromere position, are the percentages of the total length forming the short arms of the chromosomes. The 95% confidence limits for each length or percentage length are also shown. The dark lines at the ends, and also within some chromosomes, are the positions of bands shown up by Giemsa staining (from de Vries and Jongerius, 1988).

sets of possible variants or 'alleles' for each gene, carries four such alleles. This makes the study of genetics, including the identification of which variants or alleles occur for each gene, more complicated than for diploids. Chromosome numbers of 32 (tetraploids) and sometimes 24 (triploids) also occur in chives and rakkyo, and Chinese chives are commonly tetraploid (Havey, 2002).

In onion, chromosome segments throughout the length of the chromosome arms can cross over during meiosis whereas, in Japanese bunching onion, crossover points are restricted to a region close to the centromere on each chromosome (Havey, 2002). The same restriction of crossing over occurs in leeks and gives rise to the characteristic cross-shaped patterns in the paired chromosomes seen in meiosis (see Fig. 3.2). It is thought that the localization of crossing over to this short section of the chromosomes in leeks prevents the association of more than two chromosomes during leek meiosis (Jones, 1990). Otherwise, association and crossing over between groups of three or even four similar chromosomes might occur, and thus prevent the normal separation of equivalent pairs of chromosomes to each daughter nucleus in the later stages of meiosis. Such irregularities usually result in infertility. Therefore, this localization of crossing over in leek probably preserves its capacity for fertile pollen and ovule formation. Irregularities of pairing in meiosis resulting in unbalanced, non-viable chromosome complements in the germ cells are the cause of infertility in hybrids between allium species, as has frequently been observed in onion × Japanese bunching onion crosses.

Onion is often used in laboratory cytogenetics teaching because it has a few, very large chromosomes. These directly reflect its massive DNA content, which is 107 times more than *Arabidopsis thaliana*, the small plant with a relatively small quantity of nuclear DNA per cell and a short seed-to-seed generation time, which has, for these reasons, become the most intensively

Fig. 3.2. The 32 chromosomes of leek pairing into 16 'bivalents' during meiosis. Note that crossing over (chiasmata) between bivalents occurs only near the centromere and not at the ends of the chromosomes, hence the cross-shaped appearance of the bivalents. Scale bar = 10 μm (photograph courtesy of Dr R.N. Jones).

studied 'type' plant for genetic studies. The nuclear DNA content of onion is nearly four times more than that of barley, the nearest non-allium of a group of 11 major crop species noted by Havey (2002). The DNA content of onion is equivalent to about 15×10^9 nucleotide base pairs. Eighty three per cent of this DNA has been shown to be made up of just three repetitive fractions of DNA, the most common of which is repeated about 21,600 times. The onion genome consists of the active genes that code for proteins interspersed along the chromosomes amid much repetitive-sequence, non-coding DNA. The repetitive DNA is thought to have arisen by duplications of DNA sequences within chromosomes (Havey, 2002). Large amounts of repetitive DNA and the consequent large genome size have been correlated with slow growth and a long generation time (Meagher and Vassiliadis, 2005), features typical of most alliums, but a study comparing 75 allium species found no general correlation between genome size and life strategy within the genus (Ohri and Pistrick, 2001).

BREEDING SYSTEMS

As mentioned briefly above, several of the edible alliums are reproduced by vegetative means. Rakkyo, great-headed garlic and, in most instances, garlic are propagated from bulbs (cloves). All three species can produce inflorescences, but seed is not set and the inflorescences revert to bulbil or bulb production at various stages of development, except in the case of a few, recently discovered fertile garlic clones. Chinese chives flower and produce viable seed but normally, during egg cell formation, the chromosomes double and a complete set of 32 mother plant chromosomes enters the egg cell. There is, therefore, no fertilization and recombination, and the outcome is genetically equivalent to vegetative reproduction – this is termed apomixis. Hybridization occurs in about 10% of the offspring of crosses between cultivars of Chinese chives (Kojima *et al.*, 1991), so a low percentage of normal fertilization and gene exchange can occur. Pollination, although not usually resulting in fertilization, is necessary for seed production, since the nutritive seed endosperm tissue fails to form without pollination (Kojima and Kawaguchi, 1989).

Clones of garlic that can produce viable seed following normal meiosis, pollen formation and fertilization were discovered in the centre of origin of the crop in central Asia. Selection from these clones has resulted in improvements in fertility, seed yield and germination rate, and a reduction in seedling defects (Etoh and Simon, 2002). Using these clones, genetic studies on garlic are now possible (Zewdie *et al.*, 2005). Many strains of shallot are also maintained vegetatively, but in recent years seed-propagated cultivars developed in Israel and The Netherlands have been of growing importance (Rabinowitch and Kamenetsky, 2002).

Despite the lack of genetic recombination in the vegetatively propagated crops, they still show great diversity between clones. For example, clones of garlic

exist which are adapted to bulb in virtually every climatic zone from Norway to the Equator. Selections also vary in clove size and colour according to local preference. The scope for crop improvement has been restricted to the maintenance and multiplication of superior clones by vegetative means (Messiaen *et al.*, 1993). Random genetic changes can be obtained by inducing mutations in tissue culture and raising the resulting plantlets (Novak, 1990). Although not a genetic improvement, considerable increases in vigour can be achieved by eliminating viruses from these crops (see Chapter 5).

Onion, Japanese bunching onion, leeks and chives all produce fertile flowers and are normally predominantly cross-pollinated. These plants are, however, perfectly capable of self-pollination. In all these species the anthers of individual flowers ripen and shed their pollen before the stigmas are fully receptive (see Fig. 2.17b and c) – this is termed protandry (Currah, 1990). In wild alliums, which have only a few flowers per flower head, this is probably an effective barrier to self-pollination. However, the vegetable species can have up to 1000 individual flowers per umbel and, because the opening of different flowers may spread over 2 to 4 weeks, it is easy for pollen to fertilize the receptive stigma of a more advanced flower on the same flower head. Therefore, protandry offers only a partial barrier to self-pollination. Typically 75–90% of seeds result from cross-pollination in onion seed fields, and leeks are normally more than 80% cross-pollinated. In certain conditions, for example in the mesh cages used by plant breeders to isolate plants from stray insects carrying unwanted pollen, the degree of cross-pollination may decrease to only 23–56% because bees and flies are often less active in these conditions.

In all these species the vigour and survival rate of seedlings derived from self-pollination (termed 'selfs') are much lower than from cross-pollination. In one study, 75% of crossed onion seed survived to produce bulbs after field sowing, whereas less than 50% of selfed seed did so (Currah and Ockenden, 1983). This is a manifestation of the 'inbreeding depression' typical of cross-pollinated or 'outbreeding' plant species. In a comparison of onions inbred by one generation of selfing with ordinary open-pollinated populations, the average bulb yield of several inbreds was only 64% of that of the open-pollinated populations, the mean maturity date was delayed by 12 days and thick-necked bulbs increased from 2 to 12% (Dowker and Fennell, 1981). After three generations of onion selfing, plant survival rates may be down to 50%, and low vigour results in only 70% of the survivors being capable of producing seeds (Jones and Mann, 1963). In a trial with leeks, mean plant weights were decreased by 35% by one generation of inbreeding and by 60% by two generations of selfing (Pink, 1992). Because of this severe inbreeding depression, seed derived wholly from cross-pollination has a higher survival and yield potential than seed from an open-pollinated seed crop, which always contains a proportion of selfs. One of the benefits of using hybrid cultivars (see below) is simply that they guarantee that all the seed sown derives from cross-pollination.

GENETICS

Compared with many crop species only a small number of 'qualitative' genes with easily visible effects have been described in onion. One example is a recessive gene which, when homozygous, results in dwarf seedstalks. In the heterozygous condition the seedstalks are of normal length because the allele for normal length is dominant over that for dwarf. Genetic analyses of onions are time-consuming because of the biennial generation time and the severe inbreeding depression, which means that it is difficult to produce and maintain a large number of near-homozygous inbred lines ideal for genetic linkage analysis. King *et al.* (1998) stated that just 17 morphological or disease-resistance gene loci had been described for onion, including those for: colours of bulbs, foliage, anthers and seedcoats; male fertility restoration in cytoplasmic male-sterility; pink-root resistance; ozone damage resistance; dwarf seedstalk; and four loci deleterious for chlorophyll.

The colour of onion skins is determined by the combined effect of a number of major genes, each of which has different alleles causing well-defined qualitative effects (El-Shafie and Davis, 1967). This is a good example of 'epistasis', an important genetic phenomenon where the interaction of several different genes determines the outcome, in this case of whether the onion bulb has a white, yellow or red skin. Many of these epistatic effects have now been explained in molecular terms. They provide elegant examples of how changes in chromosomal DNA sequences result in modifications of gene control, enzyme synthesis or enzyme function to modify a biosynthetic pathway and thereby the resulting plant (the 'phenotype'). Five major genes affecting bulb colour were discovered by classic genetic inheritance studies. The interactions between these genes imply that they act sequentially along the biosynthetic pathway for anthocyanin pigments (see Fig 3.3; Kim *et al.*, 2004b, 2005a; Chapter 8, this volume).

First, this pathway depends on the basic colour factor or C gene, which has both dominant and recessive alleles. White-skinned onions lack the enzyme chalcone synthase (CHS), so that they do not produce any pigments of the anthocyanin pathway (see Fig 3.3). The C gene appears to be a regulatory gene that controls whether or not the genes coding for two CHS enzymes actually transcribe and initiate the process to synthesize the enzyme proteins (Kim *et al.*, 2005b). Yellow onions from the USA have a deletion in the DNA of the gene that that transcribes for the enzyme dihydroflavonol 4-reductase (DFR) (see Fig 3.3; Kim *et al.*, 2004a). This mutation prevents the production of DFR and therefore blocks the pathway after dihydroquercetin, resulting in the accumulation of the yellow quercetin pigment without any red cyanidin.

Brazilian yellow onions do produce DFR and also the anthocyanidin synthase (ANS) protein (see Fig 3.3), but a point nucleotide mutation in the DNA sequence coding for ANS results in the substitution of the amino acid glycine by arginine at the corresponding point in the amino acid sequence of the enzyme.

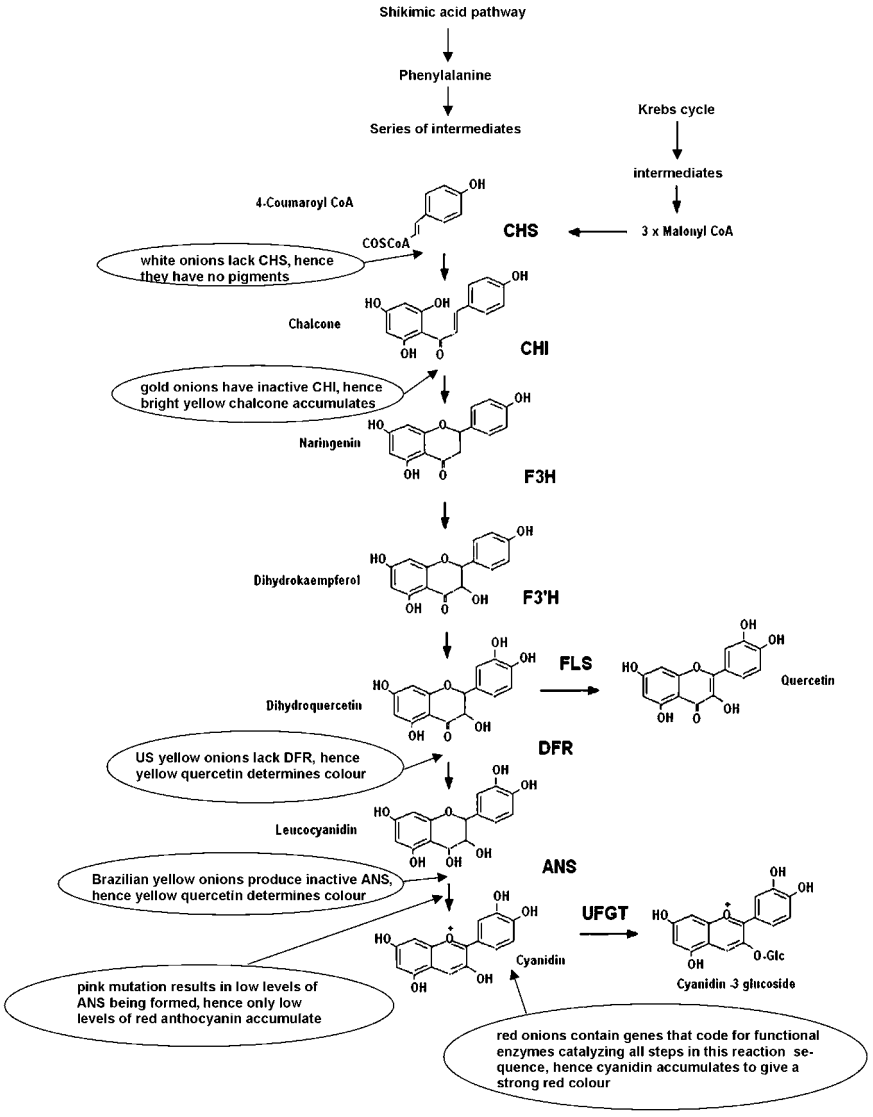


Fig. 3.3. The anthocyanin pigments biosynthesis pathway in onions showing how the gene alleles that determine skin colour act at the enzyme level to determine which pigments are produced. The enzymes are abbreviated as follows: CHS, chalcone synthase; CHI, chalcone isomerase; F3H, flavanone 3-hydroxylase; F3'H, flavonoid 3'-hydroxylase; DFR, dihydroflavonol 4-reductase; ANS, anthocyanidin synthase; FLS, flavonol synthase; UFGT, UDP glucose-flavonoid 3-*o*-glucosyl transferase (annotated from Kim *et al.*, 2004b. Courtesy of *Molecular Genetics and Genomics*).

The arginine substitution is close to an active binding site in the enzyme and this probably causes its inactivation, hence blocking anthocyanidin synthesis (Kim *et al.*, 2005a). Crosses between US and Brazilian yellow onions result in some red onions, since some of the offspring inherit the alleles producing normal DFR from the Brazilian parent along with alleles for functioning ANS from the US parent, thereby allowing the biosynthetic pathway to cyanidin to function (see Fig 3.3). This explains the long-recognized 'complementary gene effect', where the interaction of two gene loci could result in red-skinned offspring from crosses between two yellow-skinned parents (El Shafie and Davis, 1967).

Another gene variant found in some unusual gold-coloured onions involved a small DNA change that resulted in the production of inactive chalcone isomerase (CHI). The consequent block in flavonoid biosynthesis resulted in the accumulation of the bright yellow pigment chalcone (see Fig 3.3; Kim *et al.*, 2004b). Another allele produces low levels of ANS (see Fig. 3.3), resulting in less cyanidin production and leading to pink rather than red bulbs. This is thought to be a result of changes in a regulatory sequence of DNA adjacent to the sequence actually coding for the ANS protein (Kim *et al.*, 2005a).

The influence of qualitative genes with discrete major effects is often enhanced or reduced by a number of minor modifier genes with a quantitative influence. This is so for the major gene for seed stalk length described above, and also for the gene that confers resistance to pink root disease in onion. Twenty qualitative genes identified in edible alliums were listed by Rabinowitch (1988). In more recent years, with application of molecular genetics to the alliums, gene loci are being identified more rapidly. These include genetic loci for the enzymes affecting bulb colour discussed above, for several sulfur-metabolism enzymes involved in the synthesis of flavour compounds and for a key enzyme in fructan biosynthesis (McCallum *et al.*, 2005a, b, 2006; Chapter 8, this volume). The DNA sequences of the genes that code several of these enzymes have been determined, and this information is helping to clarify the structure and function of the enzymes (Shaw *et al.*, 2005). A genetic locus for mildew resistance has been identified from wild alliums and is being introduced into onion (see Breeding for Disease and Pest Resistance, below). Shigyo and his colleagues have reported genetic loci for ten enzymes of carbohydrate and amino acid metabolism, using different variants of the enzymes (isozymes) for the genetic analyses and to locate on which chromosome the loci occur (Shigyo *et al.*, 1996; van Heusden *et al.*, 2000a).

In addition to the identification of genes for individual discrete traits or enzymes, groupings of genes or polygenic regions controlling various aspects of biochemistry have been located to particular chromosomes or genetic linkage regions. These include the regions coding for fructans (Havey *et* al., 2004), flavour compounds (Galmarini *et al.*, 2001), sugar content in leaves (Tran Thi Minh Hang *et al.*, 2004) and flavonoids and anthocyanins in leaf sheaths and some of the enzymes involved in their synthesis (Shigyo *et al.*, 1997; Masuzaki *et al.*, 2006). In addition there are 2608 published sequences of DNA from onion

that express as RNA in roots, shoots or callus and which have correspondences with genes of known function in other organisms (Kuhl, *et al.*, 2004; see Genomics, below).

The majority of traits, including most of those important for crop productivity, are controlled by the combined effects of a number of genes that influence the trait, each of which has a similar, small, 'quantitative' influence. For example, yield, maturity date and ease of bolting are each conditioned by the additive effects of several genes. Thus, crosses between extreme types for maturity date give hybrids intermediate to the parents but, from the hybrids a continuous range, rather than a few distinct classes, of maturity dates are derived in later generations. The aim of breeding is to combine together in the complement of genes, or 'genotype' of a variety, alleles that are favourable for desired quantitative traits. For example, the genotype should contain all the favourable alleles for the genes that determine high yield either homozygously or, if these alleles are dominant over complementary alleles conditioning lower yields, the presence of the favourable dominant as a heterozygote is equally good.

A high level of heterozygosity exists in onion populations sustained by generations of random outcrossing. This allows deleterious recessive alleles to perpetuate in the genetic pool. Self-pollination results in homozygosity for a high proportion of these recessive alleles, thus manifesting their effect and causing the inbreeding depression described above. Prominent among the deleterious recessives are those causing chlorophyll deficiency. In one survey 20–30% of plants were heterozygous for a chlorophyll deficiency recessive allele and approximately 20 such gene loci were estimated to be present in onion populations (Berninger and Buret, 1967).

Because leeks are tetraploid and therefore carry four alleles for each gene, there is even more scope for deleterious recessive alleles to be carried in heterozygous genotypes than with a diploid such as onion. Between seven and 14 different chlorophyll deficiency genes have been found in leeks and, in an open-pollinated population, it was estimated that more than 60% of plants were carrying two copies of such deficiency alleles in one or more such genes (Berninger and Buret, 1967). Leeks are subject to severe inbreeding depression.

GENETIC LINKAGE MAPS

Following a cross between two parents carrying contrasting alleles at a range of gene loci, the inheritance of the alleles for each locus can be followed in subsequent generations. If two characteristics conditioned by two different genetic loci are inherited independently they are said to be 'unlinked', and the gene loci can be assumed to be located on different chromosomes. If, in contrast, the inheritance of the two characteristics shows some correlation and not just random association, their gene loci are said to be 'linked' and they can normally be assumed to be on the

same chromosome. The degree to which the two characteristics are inherited together, in other words the strength of the linkage, can be quantified. Characteristics that rarely recombine can be assumed to be controlled by genes that are very close to each other along the same chromosome, so that their alleles are rarely resorted by crossing over during meiosis.

By quantifying the frequencies of recombination between linked gene loci for a number of characteristics it is possible to order the strength of the linkages between them and construct a 'linkage map' showing their relative positions along the chromosome (see Fig. 3.4). The chromosomes are the physical reality

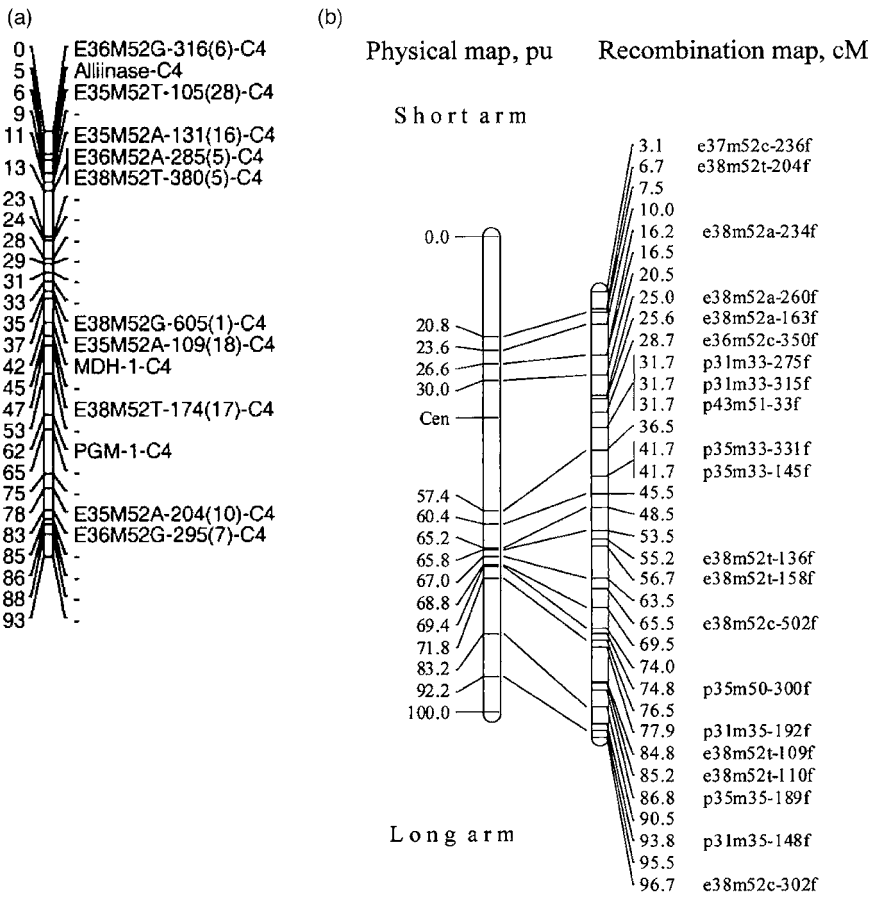
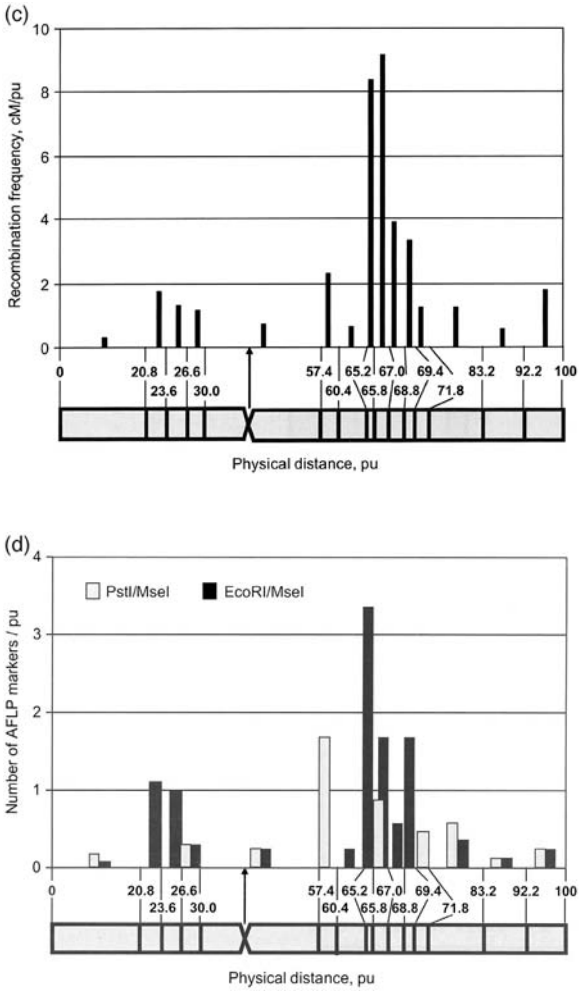


Fig. 3.4. Genetic maps of alliums. (a) A linkage map of *A. cepa* (shallot) chromosome 4. The long codenames apply to DNA markers of the Amplified Fragment Length Polymorphism (AFLP) type that was used for map construction. The locations of the genes coding for the enzymes alliinase, malate dehydrogenase (MDH) and phosphoglucomutase (PGM) are shown on the map (part of Fig. 2 of



van Heusden *et al.,* 2000b. Courtesy of *Theoretical and Applied Genetics*). (b) The integrated physical and recombination map of *A. fistulosum* chromosome 8. The AFLP marker linkage map is on the right and the physical locations of the markers along the chromosome are shown on the left in terms of percentages of the total chromosome length (part of Fig. 3 of Khrustaleva *et al.,* 2005. Courtesy of *Genetics*). (c) The physical distribution of recombination frequency along chromosome 8 of a recombinant hybrid between *A. fistulosum* and *A. roylei*. The black arrow indicates the position of the centromere (Fig. 5 of Khrustaleva *et al.,* 2005. Courtesy of *Genetics*). (d) The density of occurrence of AFLP markers along a recombinant *A. fistulosum* × *A. roylei* chromosome 8. Two sorts of markers are shown corresponding to two types of restriction enzyme combinations used to derive markers. The PstI/MseI markers probably correspond with areas of actively expressed genes (Fig. 7 of Khrustaleva *et al.,* 2005. Courtesy of *Genetics*).

underlying a linkage map derived from inheritance statistics. Separate 'linkage groups' of characteristics that are inherited together, each corresponding to a different chromosome, should result from a linkage map based on many characteristics. The independent inheritance of characteristics determined by genes in different linkage groups reflects the random assortment of the two segregants from each chromosome going to each daughter cell during meiosis. Considerable research effort is now being devoted to the development of genetic linkage maps for the edible alliums, particularly onion, as reviewed in McCallum (2007) and Havey *et al.* (In press).

The first genetic maps were based on the inheritance of easily observable characteristics but, as we have seen, there are relatively few of these known for alliums. Moreover, some of the observable characteristics, like disease resistance, need considerable effort to assess. Nowadays, genetic maps are based primarily on molecular 'markers', which can be found in large numbers and which can be rapidly detected using techniques of molecular biology. One of the useful outcomes of such work is that the inheritance in plant breeding lines of important properties that need much effort to assess – for example, disease resistance or the *Ms* genes for fertility restoration (see below; Gokce *et al.*, 2002) – can be followed easily by using molecular markers closely linked to a desired trait to rapidly and cheaply detect its presence or absence in individual plants in a breeding programme. Often, such tests can be done at the seedling stage, so that only individuals retaining alleles for a desired trait need be grown on. This is termed 'marker-assisted breeding'. Molecular markers used in the genetic mapping of alliums were described by Klaas and Friesen (2002). Briefly, molecular markers group into isoenzymes and DNA-based techniques. Isozymes are allelic variants of particular enzymes that can be distinguished and followed in inheritance studies (Shigyo *et al.*, 1996).

DNA-based techniques break down into a number of subcategories. First there are techniques based on differences in the sizes of DNA fragments. These are generated by applying a succession of cleaving enzymes to the DNA. Genotypes may differ in the resulting size of DNA fragments from a particular point along the chromosomes, and the inheritance of these differences in size fragments can be followed. Secondly there are techniques based on DNA sequence differences that vary between genotypes. For example, there may be sequence repeats, nucleotide omissions or nucleotide substitutions. These molecular variants that show up as detectable DNA differences at the same location along the homologous chromosomes are called polymorphisms. The inheritance of the different variants within a polymorphism can be followed, just as can the inheritance of different alleles for contrasting forms of a visible attribute like long or short flower stalks.

The first linkage map of onion was based on DNA polymorphisms and has 114 loci located over 12 linkage groups (King *et al.*, 1998). It was derived by following the inheritance of the DNA markers in 58 third-generation families of controlled crosses and selfs derived from an original cross between an inbred

line from the low-pungency, low-soluble solid cv. 'Ailsa Craig' and an inbred from the higher-pungency and soluble solid cv. 'Brigham Yellow Globe'. Alleles for male fertility restoration, a complementary gene for red bulb colour (see previous section) and the enzyme coding for alliinase (see Fig. 8.2) were located on the linkage map and associated with neighbouring DNA markers. A subsequent analysis of this cross followed the inheritance of DNA markers in parallel with differences in sugar and fructan (see Chapter 8) content deriving from the parent lines. Results showed chromosome regions on linkage groups A, D and E to be associated with the control of fructan content (Havey *et al.*, 2004).

Another genetic map based on a cross between onion and the wild species *A. roylei* discriminated 262 DNA markers on the onion genome into eight linkage groups (van Heusden *et al.*, 2000b). A gene for alliinase and the location of a gene for resistance to downy mildew disease derived from *A. roylei* were located by this map. Linkage groups in this map were later assigned to the individual physical chromosomes of *A. cepa* (see Fig. 3.4a; van Heusden *et al.*, 2000a). This was done using molecular markers for *A. cepa* that could be located in the *A. cepa* × *A. roylei* linkage map and also in chromosomes derived from *A. cepa* in a set of eight lines of bunching onion, *A. fistulosum*, each of which contained an extra different chromosome from shallot (*A. cepa*) (Shigyo *et al.*, 1996). These lines, termed 'monosomic addition lines', are the key to translating the linkage map into a 'physical map' located on the eight chromosomes of *A. cepa* (see Fig. 3.1). Analysis of the biochemical effects of different monosomic additions has shown that a group for flavonoid and anthocyanin biosynthesis is on chromosome 5A (Shigyo *et al.*, 1997), and genes for the production of sugars in leaves on chromosomes 2A and 8A (Tran Thi Minh Hang *et al.*, 2004).

A further refinement has been to compare 'genetic distances' between DNA markers – as shown by linkage maps – with the physical distance between markers along the chromosomes by direct visualization and position measurement of meiotic crossing over, using a refined staining technique, in parallel with the recombination mapping of markers (see Fig. 3.4; Khrustaleva *et al.*, 2005). Recombination frequency varied in different regions along the chromosome, indicating that the 'genetic distances' between markers correspond to variable physical distances along the chromosome (see Fig. 3.4c). The pattern of variation of recombination frequency was different to that found for cereal crops.

DNA sequence repeat markers that can be amplified by the polymerase chain reaction (PCR) have been developed for onion (McCallum *et al.*, 2005b). Polymorphisms for these markers have been detected both between and within onion breeding lines. Onion linkage maps derived from different original parent crosses have been aligned using markers of this type to locate common points on both maps (McCallum *et al.*, 2005b). New families of inbred lines from crosses between parents with contrasting properties have been developed, so that these markers can be exploited to map the genes underlying these contrasts. Families

with more lines than the 60 or so produced so far are needed for finer-scale mapping to detect more closely linked genetic effects (McCallum *et al.*, 2005b). The development of male-fertile, seed-reproduced garlic has enabled the first genetic linkage map for garlic to be derived (Zewdie *et al.*, 2005). The genetic markers used were developed from expressed DNA sequences from onion (Kuhl *et al.*, 2004). A gene locus for fertile seed production was located on the linkage map.

Molecular markers are useful for surveys of genetic diversity both within and between allium species (Klaas and Friesen, 2002; McCallum *et al.*, 2005b). Markers are already finding practical applications within the onion industry; for example, markers from chloroplast DNA characteristic of male-sterile cytoplasm are widely used to quickly classify cytoplasm in the development of maintainer and male-sterile lines during the breeding of onion hybrids (see below) and for quality control (i.e. confirming genetic identities) in breeding and hybrid-onion seed production (Havey, 2002; Jakse *et al.*, 2005).

GENOMICS

The collection of DNA sequences and, for some organisms, the sequencing of all the genetic material, has made possible the comparison of DNA sequences within and between taxonomic groups (Havey *et al.*, in press). The function of a DNA sequence can be tentatively inferred from knowledge on what enzyme or other protein it, or similar sequences, code for in other species. Taxonomic groups showing high similarity in their arrangement of DNA subsequences along the chromosomes are said to show high synteny or colinearity.

The study of genomes investigating how they function as a whole system in controlling growth, development and adaptation – and also to clarify the phylogenetic relationships between species – is a central concern of current biological research. Such genomic studies in the alliums are in their infancy, but a library has been created of 11,008 DNA sequences derived by sequencing DNA complementary to the RNA isolated from bulb, root, leaf and callus tissue of onion (Kuhl *et al.*, 2004). The sequence information is freely available online at http://compbio.dfci.harvard.edu/tgi/cgi-bin/tgi/gimain.pl?gudb=onion.

Since they are derived from RNA found in the tissues, these are the DNA sequences that are actively transcribing for RNA and hence they are termed 'expressed sequence tags' (EST). They should encompass the active genes in their respective tissues. Sixty per cent of these sequences matched proteins from other organisms, of which nearly 24% could be tentatively assigned to some gene functionality, mostly involved with metabolism. EST markers showing similarities to EST markers from rice were selected and linkage mapped using the lines derived from the 'Ailsa Craig' × 'Brigham Yellow Globe' cross mentioned above under linkage maps. Physical locations for these markers on the chromosome were determined using the monosomic addition lines also

mentioned above. A comparison of the ordering of these ESTs in onion with that known for rice showed little similarity (i.e. scant colinearity). These results suggest that genomic information from the grass family crops (Order Poales), of which there is a vast amount, may not provide appropriate genomic models for crops in the Asparagales Order – e.g. alliums (Martin *et al.*, 2005).

This makes it necessary to develop more genomic information for these plants. In view of the large genome and long generation time for onions and other vegetable alliums, a species in the Asparagales with a smaller genome and short life cycle is likely to be chosen as a 'model' for developing a detailed genetic map applicable to the Order. The expected large measure of colinearity of genes between the genomes of different species within an order would facilitate the application of genomic information from such a 'model' species to the crop species. As information is published on allium genetic sequences by research groups worldwide, it is being collated at the above web site so that genomic information is accumulating in a coordinated and collaborative way (Havey *et al.*, in press).

HYBRID VIGOUR

Crosses between widely divergent onion populations can produce hybrids that exceed either parent in vigour. For example, Synnevag (1988) crossed a Finnish multiplier onion with a Norwegian large-bulbed cultivar and obtained hybrids that outyielded either parent yet had a shorter growing period than the large-bulbed parent. Such an effect is termed 'hybrid vigour' or 'heterosis'. In such hybrids the influence of any unfavourable recessive alleles homozygous in the parent lines may be masked by more favourable dominant alleles from the other parent. When a number of parent lines are crossed, even if they are themselves weak and inbred, some of the resulting hybrids can be extremely vigorous, and may even exceed the performance of a vigorous cross-pollinated line. The fixing of genotypes showing such hybrid vigour in F_1 hybrid cultivars has become the dominant trend in onion breeding in recent years. Such hybrids have also been developed in Japanese bunching onion, chives and leeks. From a commercial point of view, one advantage of F_1 hybrids is that they will not breed true from saved seed, but must be produced anew every generation from the appropriate parent lines, which remain under the control of the breeder or seed company.

GENETIC MALE STERILITY AND HYBRID BREEDING

The most important qualitative genes in the edible alliums are those that cause male sterility. In male-sterile plants pollen fails to develop and they are therefore incapable of self-pollination. Hence, any seed produced must result from cross-pollination. This property has been utilized to produce F_1 hybrid cultivars

showing hybrid vigour, hence the importance of these genes for plant breeding. In the absence of male sterility, controlled cross-pollination without any self-pollination can be achieved only by laboriously removing ripening anthers from a flower head before they shed pollen, and by then transferring the desired crossed pollen to the stigmas by hand. Such a procedure is too labour intensive for anything but a few controlled crosses in breeding or experimental work.

In onions, male sterility was first exploited by Jones and Clarke using a male-sterile specimen of cv. 'Italian Red', which they found in breeding plots at Davis, California in 1925. Fortunately, when this plant was prevented from being cross-pollinated, bulbils were produced in the flower head (see Fig. 4.41) and it could be propagated. Jones and Clarke (1943) published a classic paper describing the genetics of male sterility and indicating how it could be used to produce hybrid cultivars. On the basis of these techniques, originally developed in onions, male sterility has since been exploited in hybrid breeding in several other important crops.

Male sterility in onion was shown to depend on the combined effects of a nuclear (i.e. chromosomal) gene and a cytoplasmic factor. The nuclear gene has two forms, the dominant *Ms* form which, when present, always results in fertile pollen, and the recessive *ms* form which, if homozygous, may result in sterile pollen. Homozygous *ms* genotypes cause male sterility only if they are combined with the cytoplasmic sterility factor S. The cytoplasm of the egg cell can carry the factor S, allowing *msms* genotypes to express as sterile or it can carry the factor N, which always results in a plant with fertile pollen, irrespective of the *ms* and *Ms* allele content of its nuclear genes.

Three genotypes for the male-sterility gene can exist in a diploid onion: *MsMs*, *Msms* and *msms*. Each of these genotypes can occur in cytoplasm carrying either the N or the S factor. The only combination that results in male sterility is *Smsms*. The cytoplasmic factor (S) is transmitted only via the female (pistillate) parent in a cross – it cannot be transmitted by pollen.

If a male-sterile mother plant is pollinated by the various possible fertile pollen donor genotypes the results will be as shown in Table 3.1.

A second source of cytopasmic male sterility (CMS), called T cytoplasm, was discovered in France and is now used for producing some European and Japanese hybrid onions. Plants with T cytoplasm are fertile if they have the dominant fertility-restoring allele A or both of two dominant alleles C and D for two complementary genes that act together to restore fertility (Havey, 2002). More recently, cytoplasmic male sterility has been introduced into onion by crossing with the wild-species *A. galanthum*. Fertility can be restored by a dominant allele at one gene locus and it has been shown that this is not the same restorer gene as for the S type CMS detailed above (Havey, 2002; Kik, 2002). These alternatives should avoid dependence on a single genetic source of CMS in hybrid onion breeding. This reduces the risk of disease susceptibility linked to CMS in all hybrids, such as occurred for southern corn blight in hybrid maize in the 1960s.

Table 3.1. The outcomes when a male-sterile onion is pollinated by the various possible male-fertile genotypes.

Mother plant (male-sterile)	Pollen donor (male-fertile)	F_1 Offspring (only the third combination results in all male-sterile offspring)
Smsms	NMsMs	All SMsms, male-fertile
Smsms	NMsms	SMsms, male-fertile; Smsms, male-sterile
Smsms	Nmsms	All Smsms, male-sterile
Smsms	SMsMs	All SMsms, male-fertile
Smsms	SMsms	SMsms, male-fertile; Smsms, male-sterile

Plants with male sterility-inducing S cytoplasm and fertility-restoring N cytoplasm can be distinguished by various molecular markers from the DNA in their chloroplasts (Havey, 2002). One of these – the ability to amplify a section of chloroplast DNA specific to N cytoplasm using the polymerase chain reaction (PCR) supplied with appropriate oligonucleotide primers – has been developed into a rapid test to distinguish N- from S-type cytoplasm. To establish a plant's cytoplasm type by conventional cross-breeding would take 4–8 years. These oligonucleotide primers are now used quickly and cheaply to classify cytoplasms for maintainer and male-sterile breeding lines. They are also used for quality control of hybrid onion seed-lots, all of which should have S-type cytoplasm (Havey, 2002).

Analogous systems of male sterility, conditioned by the combination of a cytoplasmic factor and a major gene factor, have been found in Japanese bunching onion and chives (Havey, 2002); in both these crops the system has been exploited to develop hybrid cultivars. In chives, the cytoplasmic sterility factor has been shown to be carried by the mitochondria. In leeks, genes for male sterility have been found, but a cytoplasmic male sterility factor has not been identified. The T-type CMS of onion has been transferred to leek in experimental hybrids between the two species and normal, vigorous growth of offspring with the onion T cytoplasm and leek chromosomes was observed, provided chromosome 1C from onion was also present (Peterka *et al.*, 2005). A vigorous male sterile line that was easily propagated from bulbils formed in the umbel was crossed with several cultivars of leek to produce high-yielding hybrids (Smith and Crowther, 1995). Variability in plant weight in these hybrids was about half that in the parent varieties, mainly because weak, selfed seedlings cannot occur. F_1 hybrid cvs of this type are growing in popularity because of their improved uniformity and higher yields (de Clercq and van Bockstaele, 2002).

TECHNIQUES OF BREEDING AND CULTIVAR IMPROVEMENT

Programmes of crop improvement currently used for edible alliums include: (i) the simple selection of desirable individual plants from a population for use in

intercrossing and seed production; (ii) the use of replicated trials and statistically based measurements of the average performance of different lines or families in a breeding programme to choose those to be retained and combined in an improved cultivar; and (iii) the development of F_1 and triple-cross hybrid cultivars. The most appropriate technique depends on how well developed the existing cultivars are, and on the expertise and resources available for breeding. The following examples of actual onion breeding programmes illustrate these various approaches. These breeding methods are summarized in Fig. 3.5.

Mass selection

Currah (1985) described a breeding programme to develop onion cultivars suitable for Ethiopia from rather variable Sudanese cultivars. Approximately 2000 bulbs were produced and selected to eliminate off-colour, double, thick-necked and small bulbs from within red-, brown- and white-bulbed populations. About half of the bulbs were saved from each sowing, although in most such programmes only 1–5% of plants would be selected. These were replanted and allowed to flower and cross-pollinate within the population of each colour. The seed was collected and resown as soon as ripe and the whole process was repeated annually. In most climates a biennial cycle with bulb production in year 1 and seed production in year 2 is necessary. Five such cycles were sufficient to develop an improved cultivar of each colour that was capable of producing export-quality bulbs. This breeding technique is known as 'mass selection'.

Continuing selection of bulbs during routine seed production is essential in maintaining the quality of such cultivars. Mass selection is effective where, as in this case, a fairly large shift is needed to adapt a breeding population to a new locality and, in consequence, off-types are numerous and obvious. Mass selection was probably widely used for developing open-pollinated European onion varieties until the 1980s (Dowker *et al.*, 1984). Mass selection is simple, requires little specialized knowledge of plant breeding and so is suitable where there is little expertise or technology available. Where populations are already highly bred and improved, however, it becomes difficult to advance by such simple techniques.

Line selection

The breeding of improved open-pollinated onion populations in the UK was described by Dowker *et al.* (1984). A fairly wide range of northern European cultivars were selfed and inbred for one to three generations. The resulting inbred lines were grown in replicated trials and the bulbs were assessed for: (i) appearance (skin retention, skin colour and shape); (ii) yield (including an allowance for the proportion of thick-necked plants and maturity date); and

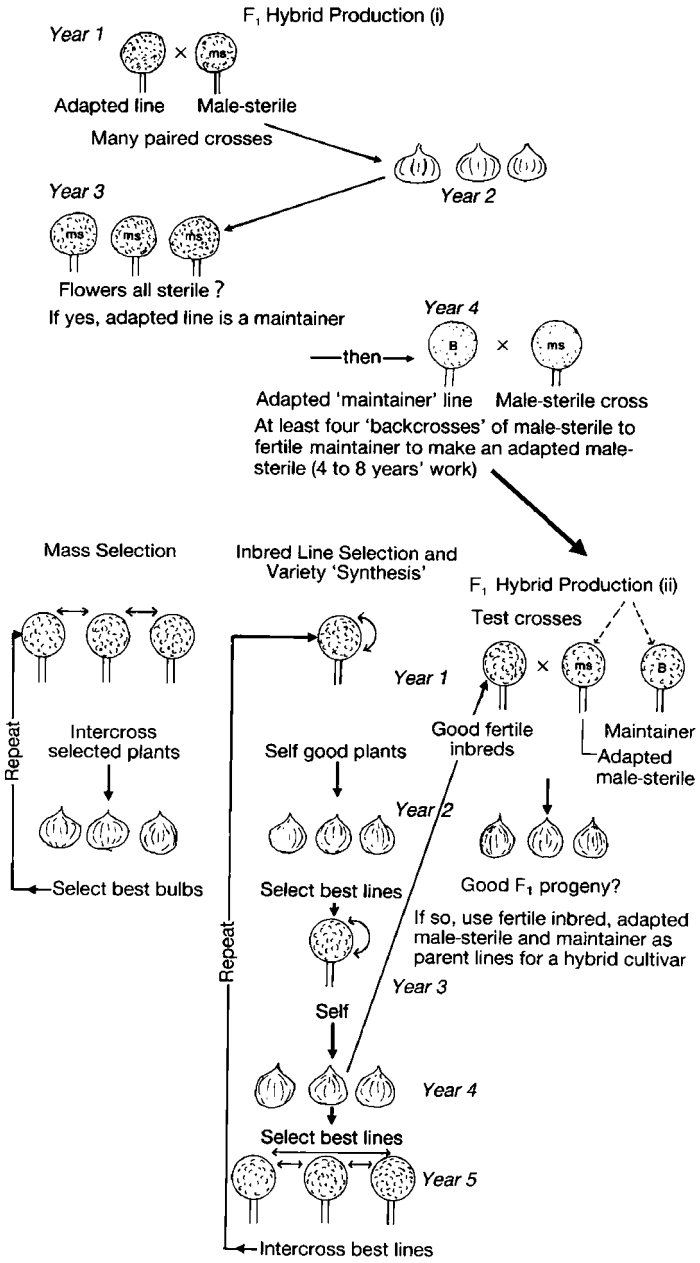


Fig. 3.5. A summary diagram of the breeding techniques used to develop new onion cultivars. (i) The first stage of breeding hybrids: producing male-sterile and maintainer lines from locally adapted types. (ii) Parallel stages in improvement by mass selection, the development of 'synthetic' cultivars or by breeding hybrid cultivars.

(iii) storage life. Selected lines were then intercrossed to make a new 'synthetic' outbreeding population. Selection was based on the average performance of the inbred lines rather than on individual bulbs. Those lines that were significantly better than a control cultivar in at least one set of properties, and not significantly worse for any other, were intercrossed. The control was one of the original well-adapted cultivars used as starting material. Equal weights of seed saved from each parent in the intercross were bulked and grown to bulb, and plants from 100 selected bulbs were mass pollinated to bulk-up the seed of the resulting 'synthetic variety' for use in trials replicated at three locations. The cycle of inbreeding and selection and synthesis was then repeated, using the population from the first cycle as a starting point.

Yields were increased by 5.5%, and the percentage of bulbs sprouting in store by April decreased by 7.5%, per cycle. The yield improvements were similar to those reported for maize under a similar breeding regime. This kind of selection programme can be fairly 'open-ended'. The number of generations of inbreeding and the number of cycles of selection can vary, and promising new lines can be brought into the sequence at any stage (Dowker, 1990). As well as inbreds, lines that are partial inbreds – like the half-sibs that result from growing the seed from a single mother plant in isolation – can also be used as 'lines' in such a programme. Line selection has replaced mass selection in leeks from the 1960s onwards and has led to modern cvs largely replacing the older, mass-selected landraces (de Clercq and van Bockstaele, 2002).

Hybrids

If a particular male-sterile line crosses with a particular pollen donor to produce a vigorous F_1 hybrid with desirable traits, then we have produced a hybrid cultivar. To reach this point usually involves many years of careful work.

First, there is the problem of how to reproduce a male-sterile mother line incapable of pollinating itself. In early work Jones and Clarke maintained their male-sterile vegetatively using the bulbils produced on the flower head. However, bulbils are difficult to store and viruses tend to accumulate in the plants. To overcome these problems they developed male-fertile 'maintainer lines' with the genetic constitution *Nmsms* for male sterility but, in other respects, genetically near the same as the male-sterile line. Such a line will, as shown above, produce pollen that can fertilize the *Smsms* male-sterile line, the offspring will remain *Smsms* and therefore male-sterile but will not vary otherwise genetically from the parent male-sterile. Thus, the *Nmsms* line makes it possible to produce successive generations of seeds of the male-sterile line, hence its name 'maintainer line'.

Male-sterile and maintainer lines must be developed, which have the potential to produce good hybrids. This means that these lines must be well adapted to the locality where the hybrid is to be grown. Male-sterile plants have

been found at a very low frequency in a number of onion populations. Also, plants with the constitution *Nmsms*, i.e. maintainer genotypes, occur with a frequency of about 5% in most populations (Pike, 1986). If the cross between such a male-sterile discovery and a fertile plant gives offspring that are all male-sterile, the breeder immediately has a new male-sterile and maintainer line. Normally, however, new male-sterile lines must be developed utilizing a known male-sterile from a non-adapted source – for example, from a breeder in another locality. Such plants are crossed with a number of individuals from a locally adapted population and the progeny is grown on until flowering. Any such cross that produces 100% male-sterile offspring serves to identify the original pollen donor as *Nmsms*, and therefore as a maintainer line. Normally, lines that have been inbred for one to three generations are used in such test crosses, thereby eliminating many undesirable recessive alleles from the population and increasing the homozygosity of the lines. This ensures that the ultimate hybrids produced are fairly uniform genetically and are therefore likely to be uniform in growth and development.

Once a maintainer line has been identified in a locally adapted inbred population, the male-sterile line must be developed so that it is nearly identical genetically to it, apart from the presence of the S cytoplasmic factor. This is done by repeatedly crossing the male-sterile offspring to the original *Nmsms*-adapted maintainer line. With each generation of such a cross, the genetic contribution from the original sterile *Smsms* parent is diluted by a factor of two, so that after four generations of this 'backcrossing' 96.875% of the genes in the resultant *Smsms* line derive from the original *Nmsms* line, and it is sufficiently similar to use as a male-sterile line in test crosses to identify vigorous hybrids.

Only certain crosses result in desirable F_1s, and therefore a number of adapted male-sterile and maintainer line pairs must be developed for a hybrid breeding programme to have a good chance of success. The breeder must make many crosses on to his male sterile lines and grow and evaluate the progeny to identify which give desirable hybrids. By accumulating data from such test crosses he/she can build up information which helps predict which crosses will produce good hybrids. As with maintainer lines, the pollen donor lines used to produce hybrids are usually inbred to eliminate deleterious recessive and off-type alleles from the gene pool.

Further details, including many practicalities of breeding onion hybrids with particular reference to the development of improved, short-day onion hybrids for Texas, are described by Pike (1986). The development of new hybrid onions involves a 15–20 year timescale because most seed-to-seed cycles in onion breeding involve 2 years. Seeds are sown and bulbs are selected, harvested and stored in year 1. In year 2 the selected bulbs are grown for flowering and seed production.

Because the lines contributing to hybrids are inbred, they are frequently weak and they may give a low seed yield. The potentiality for adequate seed production is essential if a hybrid is to be commercially viable. The parent lines

of a hybrid must also flower simultaneously so that they cross-pollinate. Problems of hybrid seed production are discussed in Chapter 6. If a cross is made between a male-sterile line and an unrelated maintainer line, the resulting hybrid will itself be male-sterile. Being a hybrid it may well be more vigorous than the parent lines and, consequently, it may have greater potential for seed production. This male-sterile hybrid may itself be crossed with another male-fertile line to produce what is termed a 'three-way hybrid'. The extra vigour of the male-sterile parent in a three-way hybrid makes seed production easier, but some of the genetic uniformity of an F_1 between two inbreds is lost. As with two-way hybrids, various three-way hybrid combinations must be made and trialled.

Since onion populations contain many deleterious recessive genes it is usually feasible to self-pollinate lines just two or three times before they become too weak to cultivate. Consequently, the hybrids between such inbreds are not genetically or phenotypically completely uniform. Also, since the inbred lines remain quite heterozygous, their genetic constitution may change over time by drift or selection, and this could be detrimental to the hybrid varieties they produce.

An alternative to inbreeding as a means of increasing genetic uniformity (homozygosity) is to utilize, as the parent lines for hybrid production, completely homozygous diploid plants derived by the chromosome doubling of haploid plants (Bohanec, 2002). Several seed companies are already using double-haploid lines in hybrid breeding. Haploid plants can be produced by tissue culturing unopened flowers on a gel medium containing basal mineral nutrients, sucrose and the plant growth regulators 2,4-D and BAP. Given appropriate conditions and concentrations in the culture medium, after around 100 days floral ovaries can give rise to plantlets with half the normal chromosome number, i.e. haploids (Bohanec, 2002). Some haploids undergo spontaneous chromosome doubling to produce homozygous diploid plants. The appearance of both growing plants and bulbs of both haploids and doubled-haploids is quite normal, except that haploids produce only rudimentary inflorescences, whereas flowering is normal in the diploids. The yield of haploids per 100 flowers cultured varies from 0 to 50–60% depending on the genetic make-up of the parent line, although it is usually just a few per cent in the typical outbreeding cultivars tested.

The process of haploid regeneration itself must eliminate those genotypes carrying deleterious recessive genes that would prevent a seedling from developing. However, deleterious recessives that disrupt flowering and fertility are not automatically selected out and double-haploid lines usually have low fertility. However, it should be feasible to improve fertility by cycles of intercrossing doubled haploids that are fertile, regeneration of new haploids from these crosses followed by doubling to produce diploids and their selection for fertility. Field trials comparing double-haploid lines, F_1 hybrids between double-haploids and male-sterile breeding lines, and existing open-pollinated

cultivars showed that the double-hybrids were more uniform but smaller and lower yielding than the existing cultivars (Kim *et al.*, 2007). The double-haploids mean bulb weight was 60% of the existing cultivars' mean at one trial site and 85% at another. The mean size and yield from the F_1 hybrids approached or exceeded that of existing cultivars depending on site. The use of double-haploid lines as parents for F_1 hybrids should make it possible to develop highly uniform onion cultivars expressing maximal hybrid vigour (Bohanec, 2002).

POLLINATION CONTROL IN BREEDING

It is evident from the procedures described above that the control of pollination is fundamental to breeding. In simple mass selection, the population undergoing selection must be isolated from extraneous pollen, particularly that from strains with a different bulb colour. Isolation can be achieved by producing seed in fields spaced more than 1.5 km apart. The same isolation is needed for the large-scale production of seed from open-pollinated lines produced by line selection, or in hybrid seed production. For producing smaller quantities of seed, contamination with unwanted pollen is achieved by isolating lines for crossing in insect-proof cages of nylon mesh (see Fig. 3.6a).

For controlled crosses between pairs of lines, flower heads are paired in small, mesh cages or in cellophane bags and flies are introduced to spread the pollen. Self-pollination is simply achieved by enclosing a single flower head in such a cage or bag and introducing flies (see Fig. 3.6b). On a small scale a brush can be used to hand-pollinate flowers. Controlled crossing while avoiding self-pollination can be achieved on a small scale by removing anthers from mother plants before they ripen and shed pollen, a process termed 'emasculation'.

BREEDING OBJECTIVES IN EDIBLE ALLIUMS

The knowledge of genetics and the breeding techniques discussed above are applied to move crop improvement in the direction of certain explicit goals or objectives, which the breeder must set. Some objectives, like high yield, a nutritious end-product and pest and disease resistance, are universally desirable. Others – for example, the colour and shape of onion bulbs – are determined by the preferences of the buying public. Objectives of the latter sort will often vary with locality and with the market niche identified for the improved variety. Usually, positive selection is confined to a few major traits at a time, otherwise the breeding programme becomes unmanageably large.

As described in Chapter 1, onion cultivars fall into the major categories: (i) storage types; (ii) sweet types for consumption as raw bulbs; (iii) dehydrators; and (iv) green salad types. Universally desirable traits in cultivars grown for

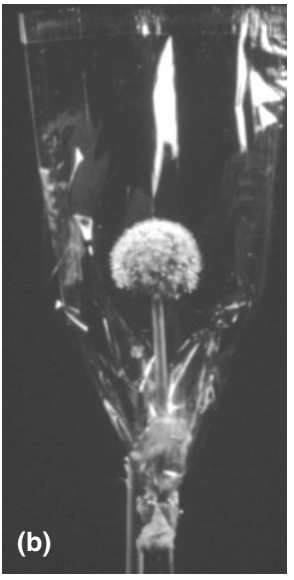


Fig. 3.6. Pollination control in onion breeding. (a) Onion umbels massed for cross-pollination within an insect-proof pollination 'cage' with nylon mesh walls. (b) Umbel enclosed by cellophane bags containing blowflies to ensure self-pollination (photographs courtesy of Warwick HRI).

bulbs are: (i) uniformity of bulb size, shape, colour and date of maturity; (ii) high yield; (iii) appropriate maturity date; (iv) disease and pest resistance; (v) bolting resistance; (vi) intact attractive skins; (vii) thin necks; (viii) single-centred bulbs (freedom from double and split bulbs); and (ix) firm flesh. To achieve many of these, the cultivar must be well adapted to the climate, principally the day-lengths and temperatures of the season and locality in which it is grown. In addition, bulbs for long storage need innately long dormancy (see Chapter 7), hard flesh, tough skins and, for most markets, pungency. Fresh bulb types should be mild-flavoured, sweet and crisp-fleshed and, here, single centres with large, concentric rings are particularly important. Dehydrators should have high dry-matter content, white flesh and skin, and low reducing sugar content. Also, spherical rather than flat bulbs are desirable for dehydrators, since this facilitates mechanical trimming of necks and roots with little loss of bulb flesh.

Examples of the more 'cosmetic' factors that tend to be culturally conditioned are the northern European preference for round, brown- or yellow-skinned bulbs, contrasting with the Japanese preference for flatter bulbs. Such preferences can change; for example, red onions are now popular in the UK, whereas in the 1980s such bulbs were rarely seen there. Since preferences vary with markets it is not possible to define fully the characteristics of an 'ideal onion'.

Messiaen *et al.* (1993) describe the objectives of garlic selection as: (i) smooth, round bulbs without visible defects; (ii) an even distribution of clove size within the bulb; (iii) a low proportion of double or multiple cloves; and (iv)

an even skin and flesh colour, which may vary from white to red or purple according to consumer preference.

Objectives for leek breeding usually emphasize a long shaft length and a dark green leaf blade in addition to high yield. In contrast to onion, leek development is not dependent on day-length and temperature, and so leek cultivars are adapted over a much wider area than onions. Climatic adaptation is a matter of having fast-growing cultivars for spring and early summer production and hardy types able to stand outside throughout the winter. Winter hardiness is usually associated with a short shaft length. Uniformity is important: leeks vary considerably in size at harvest, even after transplanting uniformly sized seedlings. With direct-drilled or module-raised crops there is a need for uniformly vigorous seedlings. Seedlings of existing leek cultivars vary in vigour, possibly because of the large number of deleterious recessive gene alleles that exist in the populations (see Genetics, above). As mentioned previously, hybrid cvs are less variable than open-pollinated cvs. Resistance to leek yellow-stripe virus and leek rust (*Puccinia allii*) are also important breeding objectives (Pink, 1992).

In recent years commercial cultivars of Japanese bunching onion have increasingly supplanted farmer-saved seed in Japan. New cultivars, including F_1 hybrids, have been bred for greater resistance to bolting, more tolerance of high temperature and improved quality. The quality objectives diverge between those grown for long pseudostems and those grown for tender green leaves (Inden and Asahira, 1990).

Plant breeding of chives has concentrated on cultivars for growing as a 'forced' crop in winter. Objectives are erect, long leaves of large diameter (> 3.6 mm), vigorous shoot branching, late flowering and high yield. F_1 hybrid cultivars have been bred that outyield open-pollinated forcing cultivars (Poulsen, 1990).

SELECTION METHODS AND ENVIRONMENTAL INFLUENCES

To select for the breeding objectives listed in the previous section, the breeder has to devise appropriate ways of measuring the characteristics selected. For some objectives he/she must ensure the trials impose a high 'selection pressure' for traits of interest. Also, efficient selection methods are dependent on knowledge of how environment influences the traits under selection. Since bulb onion development is so closely dependent on climate, it is essential that selection trials are performed in the region where it is intended to grow any improved cultivars that result.

Many objectives of onion breeding can be assessed visually and quantified by a simple scoring system. This applies to shape, colour, skin retention, skin thickness and uniformity. Maturity dates can be assessed, as when 50 or 80% of plants show collapsed foliage. The early sowing of breeding lines of overwintered crops to maximize bolting is an example of how selection pressure can be

increased above normal. Onion storage can be assessed as the percentage of bulbs sprouted or rotten after a fixed time in typical storage conditions. The soluble solids content, important in breeding cultivars for dehydration, can be assessed by a refractometer reading of juice extracted from a small plug of the bulb (see Fig. 8.7). Selected bulbs can still be used for planting. Various techniques exist for flavour assessment (see Chapter 8), but most breeders still use tasting panels. Many special tests have been devised for pest and disease resistance to supplement gross field observations (see the following section).

In the absence of continuous selection to maintain the quality of open-pollinated cultivars, some desirable features may degenerate. Continuous selection is necessary to maintain resistance to bolting, single-centred bulbs, a round bulb shape, high dry-matter content and long dormancy as, in the absence of selection, cultivars tend to 'drift' away from these ideals (Pike, 1986). Any feature that tends to increase seed yield will increase in prominence with repeated seed multiplication, in the absence of selection against it. For example, a flatter bulb shape is associated with internal branching, as are multiple centres, and both are likely to result in multiple flower heads per plant, hence an increased seed yield per plant.

All important traits are affected by environment as well as genotype. By comparing the scores from breeding lines against well-characterized control cultivars, usually grown with more replication than the lines under test, some environmental influences can be discounted. Many traits, including bulb size, shape, maturity date, the percentage of thick-necked and of double bulbs, are influenced by the population density at which plants are grown (Dowker and Fennell, 1974). The breeder should bear these trends in mind when making their selections. Bulb yield is also strongly density dependent. When onion trials are directly sown, it is impossible to achieve constant plant population densities. To overcome this difficulty, a control cultivar can be grown at a range of population densities and a mathematical relationship between yield and population density derived. Then, the yield of a breeding line can be compared with that of the control cultivar at the same population density, as predicted by this relationship (Dowker, 1990). Some breeders use transplanted seedlings grown at a fixed density to overcome the problems associated with differences of plant density. It is important to avoid the unwitting selection of the most vigorous seedlings in transplanting such a trial.

Plant density also affects important selection traits in leeks. At higher densities the ratio of shaft length to width increases, and consequently shafts appear longer and thinner. In transplanted crops, deeper planting results in longer shaft lengths.

Selection for yield in vegetatively propagated allium crops is difficult because the size of the planting material, e.g. garlic clove or shallot bulb, and also the conditions in which it was produced, e.g. plant density, affect its yield potential (Chapter 6). Simple mass selection of the largest, best-looking bulbs gives little improvement (Messiaen *et al.*, 1993). Instead, by planting cloves

from selected individual garlic bulbs, a number of clonal families were developed. Subsequently these families were planted in comparative trials and the highest yielding families were selected as those with the highest mean values of the product (weight of harvested bulb × weight multiplication between planting and harvest). The weight multiplication is simply the weight of the harvested bulb divided by the weight of the planted clove. High yielding clones are selected on the basis of several years' results from such trials (Messiaen *et al.*, 1993). For shallots it is difficult to devise a simple selection index unless mother bulbs originate from the same plot and are of similar size.

GENETIC TRANSFORMATION OF ALLIUMS

Eady (2002), in reviewing this subject, restricted the term 'genetic transformation' to the transfer of a characterized set of genes using gene insertion technologies as opposed to the introduction of non-characterized DNA from crosses with wild relatives or by the artificial fusion of cells of different allium species (Buiteveld *et al.*, 1998). To transform plants with discrete, characterized genes, the DNA sequences have to be delivered to a cell and incorporated in the chromosomes. The gene has to be regulated so that it is expressed in the desired way and the transformed cell must proliferate and generate a plantlet that can be characterized and selected as containing the inserted DNA. Finally, the selected transformed plant must be hardened-off and grown and assessed under normal cultural conditions.

Successful genetic transformation has been reported in onion, shallot, garlic and leek (Eady, 2002; Eady *et al.*, 2003a, b, 2005; Zheng *et al.*, 2004). The gene insertion system using the bacterial vector *Agrobacterium* has been most widely used. Wild-type *Agrobacterium* infects roots and transfers a specific section of DNA, known as T-DNA, into the host plant's genome. Infected cells proliferate and form a tumour that acts as a food source for the proliferating bacteria. It has been possible to suppress tumour induction and add designed sequences of DNA to *Agrobacterium* T-DNA and utilize its DNA insertion ability to incorporate coding for desired genes into plant genomes. Inserted along with the DNA required for a desired new property must be 'promoter' DNA coding for genes to regulate the novel gene, i.e. to 'switch it on' when required, and also DNA coding for 'reporter' genes. The reporter genes encode properties that enable the selection of the transformed plantlets from those with unmodified genomes, and which can be used to verify that the transformation sequence has been incorporated.

Promoters derived from both cauliflower mosaic virus and also chrysanthemum have been used in allium transformation. Herbicide resistance and antibiotic resistance genes have been used as reporters to select out the transformed cell cultures, since only those incorporating these properties can survive in growth media to which are added the appropriate antibiotic or herbicide. A gene that codes for a fluorescent protein has also been used to show

up transformed plantlets by their ability to fluoresce green when illuminated by blue light (Eady, 2002; Zheng *et al.*, 2004). The transformation process has been applied to immature embryos dissected out of developing seeds and cultured along with the *Agrobacterium* in an appropriate liquid tissue culture medium. These cultures are a source of cells that can be both transformed and regenerated. Various groups have developed systems of proliferating cells in culture suitable for genetic transformation (e.g. Fereol *et al.*, 2005). Dedifferentiated cells termed 'callus cells' are problematic for allium transformation because they can be genetically unstable and give rise to spontaneous 'somaclonal' genetic variation, and they can be difficult to regenerate into differentiated plantlets (Novak, 1990; Eady, 2002).

Using these techniques on several open-pollinated cvs and hybrid parent lines, onion plants tolerant to herbicides containing glyphosate and phosphinothricin (glufosinate) have been engineered and shown to express the genes and inherit them in a normal Mendelian way (Eady *et al.*, 2003a, b). The plants grew and bulbed normally (see Fig 3.7a). Such plants were able to withstand commercial herbicide concentrations, showing that weeds could be controlled

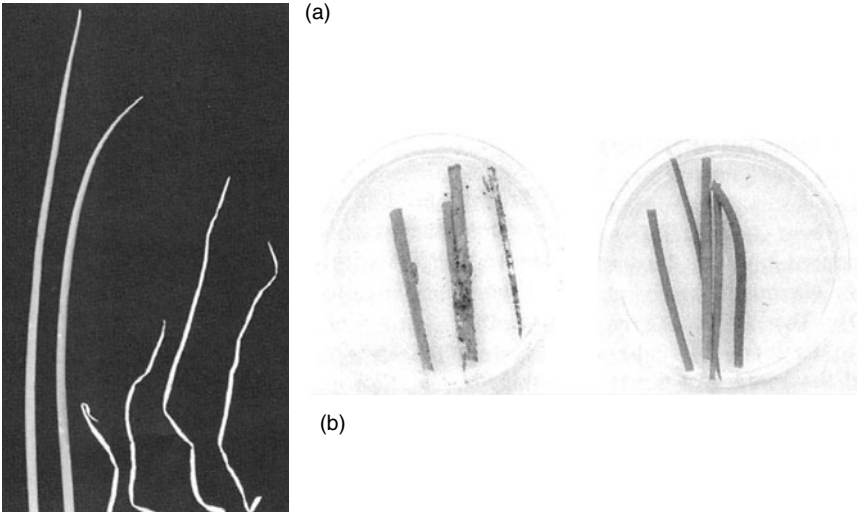


Fig. 3.7. Genetically modified onions. (a) Onion leaves 10 days after spraying with the contact herbicide phosphinothricin: (left) leaves from a *Bar*-positive plant, a genetic marker indicating the presence of the herbicide resistance gene; (right) leaves from non-transgenic plants (from Eady *et al.*, 2003b. Courtesy of *Annals of Applied Biology*). (b) (left) Non-transgenic shallot leaves exposed to the beet army worm, *Spodoptera exigua*. (right) Leaves similarly exposed from resistant plants genetically transformed to express an insect-toxic protein coded by the *cry1Ca* gene derived from *Bacillus thuringiensis* (from Zheng *et al.*, 2005. Courtesy of *Transgenic Research*).

in crops of this nature using a single, low-dose, rapidly soil-degradable, modern herbicide rather than the complex multi-herbicide pre- and post-emergence programmes presently needed. Insect resistance has also been engineered into shallot and garlic (see below). Another potentially useful transformation has been achieved by introducing an alliinase 'antisense' gene into onion. These partially block the expression of the alliinase enzyme responsible for producing flavour and aroma (see Fig. 8.2) and should therefore impact on the level of the flavour compounds (Eady, 2002).

A better technique for blocking the action of specific genes, or 'gene silencing', is RNA interference (RNAi), which is based on a powerful natural mechanism for seeking and destroying deleterious transcribed RNA, including viruses. This has been applied to develop a 'tearless' onion by suppressing the production of the enzyme lachrymatory factor synthase (LFS) that catalyses the reaction that produces the volatile lachrymatory factor when bulbs are cut (see Chapter 8; Eady, 2007).

Because genetic transformation of onion is still difficult and takes 1 year from transformation to bulb production, the LFS gene-silencing construct was first developed using tobacco plants, which are more amenable to genetic transformation. Transgenic tobacco plants producing LFS were developed, and a second transformation with an RNAi construct directed against the LFS-producing RNA was introduced and shown to suppress LFS production in the tobacco 'model' system. The LFS-suppressing genetic construct shown to work in transgenic tobacco was then introduced to onion. The introduced RNAi system seeks, dices and hence destroys specifically the RNA coding for LFS.

In this targeted way the production of the irritating lachrymatory factor is suppressed and, rather than being lost as LF, precursors should be diverted to forming more of the other flavour compounds beneficial to health (see Chapter 8). The RNAi system shows great promise for manipulating the genetic system of onions to enhance the production of nutritionally desirable secondary metabolites and for developing resistance to virus disease, as well as being a powerful tool for fundamental investigations of metabolic pathways in the plants (Eady, 2007).

BREEDING FOR DISEASE AND PEST RESISTANCE

The growing public and political pressure to minimize the use of pesticides has led to increasing emphasis on the breeding of cultivars with resistance or tolerance to disease and pest attack. Notable success in resistance breeding was achieved in controlling onion pink root, a soil-borne disease of warm regions. Early studies indicated the presence of a single recessive allele conferring resistance to this disease in Bermuda-type cultivars. This was successfully transferred to other sweet types suitable for the southern USA. Later research has indicated susceptibility to other strains of the fungus in resistant cultivars (Pike, 1986).

This illustrates the important point that resistance, particularly the sort conferred by a single gene, may break down in the face of new strains of the pathogen. Disease and pest organisms usually have short generation times and rapid rates of evolution, factors that favour the early breakdown of varietal resistance, particularly if introduced on a widespread and continuous basis. Various degrees of resistance, indicating the influence of a number of genes of small effect, have also been observed for pink root disease. Such polygenic resistance may not be as complete as single-gene resistance, but it is less liable to catastrophic breakdown in the face of a new, virulent strain of the pathogen than is single-gene resistance.

Allium fistulosum is highly resistant to pink root as well as to the other important onion diseases such as neck rot, anthracnose, smut and leaf rot due to *Botrytis squamosa* (see Table 5.5). In view of this, many interspecific hybrids between *A. fistulosum* and common onion have been produced and shown to be resistant to pink root. One or two of these hybrids are grown as bunching onions, but backcrossing the hybrids to onion to incorporate resistance into an acceptable bulb onion variety has proved difficult because the hybrids are largely sterile. This sterility results from various abnormalities in meiosis in the hybrids, and these have been analysed in considerable detail (Kik, 2002).

In an effort to overcome sterility and therefore to be able to transfer some of the disease-resistance genes found in *A. fistulosum* to *A. cepa*, some crosses between the two species have been followed by the deliberate induction of a doubling of the number of chromosomes. The resulting pairs of homologous chromosomes from *A. fistulosum* and from *A. cepa* can pair with each other during meiosis and normal crossing over, leading to viable pollen and egg cells, can occur (Jones and Mann, 1963). Such plants are termed amphidiploids, an example of which is the cv. 'Beltsville Bunching' that is grown from seed as a minor crop in the USA. An amphidiploid from a cross between a shallot and *A. fistulosum*, which was backcrossed to the shallot, gave rise to the vigorous, pink root-resistant, shallot-like 'Delta Giant', which is grown for bulbs in Louisiana. This is a triploid with 24 chromosomes, two sets of eight derived from shallot and one set from *A. fistulosum*. The oriental Wakegi onion is a diploid hybrid between shallot and *A. fistulosum*, but it is propagated vegetatively.

Several groups have demonstrated some exchange of genetic material between homologous chromosomes of the two species in backcrosses of the hybrid to *A. cepa* (Kik, 2002). More recently, it has been shown that both *A. cepa* and *A. fistulosum* will cross with the wild species *A. roylei* to produce fertile hybrids. *Allium roylei* is a diploid with an amount of DNA in the chromosomes that is intermediate between the two crop species. In a cross between *A. cepa* and an *A. fistulosum* × *Alium roylei* hybrid to form the three-way hybrid, it was possible to show that crossing over, and therefore genetic exchange, occurs between homologous chromosomes from all three species. Moreover, recombination points were randomly distributed over the chromosomes and not confined to a limited region near the centromere, as occurs in *A. fistulosum* (Kik, 2002). Thus *A. roylei* can act

as a genetic 'bridge species' that can make the introgression of useful genes from *A. fistulosum* into common onion a practical possibility.

Interest in *A. roylei* arose when it was found to be completely resistant to onion downy mildew and partially resistant to onion leaf blight, *B. squamosa*. The hybrid between *A. roylei* and *A. cepa* produced pollen with few chromosomal abnormalities and was therefore fertile, and could be backcrossed to *A. cepa*. Downy mildew resistance was shown to be due to a single dominant gene, which has been named '*Pd*' and which is located at one end of chromosome 2 in *A. roylei*. This was shown from a genetic linkage map based on molecular markers and by direct visualization of a DNA marker for the *Pd* gene on the chromosome using a fluorescent stain linked to probe DNA.

A DNA sequence of 20 base pairs closely linked to *Pd* and which can be amplified for ease of identification has been developed (termed a 'sequence-characterized amplified region' (SCAR) marker). Genetic mapping of the crosses between *A. roylei* and onion showed that the mildew resistance gene was located at the end of chromosome 3 (Scholten *et al.*, 2007). The discriminating power of the SCAR marker to show only downy mildew-resistant genotypes declined during the programme of repeated back-crossing of resistance-carrying genotypes with onion to produce resistant, good-quality onions. Hence, new AFLP markers for the resistance gene had to be developed (Scholten *et al.*, 2007). Furthermore, it was found that a region of the *A. roylei* fragment introduced into onion was lethal when homozygous within an onion genetic background.

However, one individual in which the *A. roylei* genetic fragment was shorter carried the mildew resistance gene but had lost the lethal recessive gene (Scholten *et al.*, 2007). From this, breeding lines homozygous for mildew resistance that could transmit resistance to all their progeny were developed. Several companies that have developed downy mildew-resistant onion cvs are using genetic markers to follow the incorporation of the *Pd* resistance gene into their breeding lines. This avoids having to perform time-consuming assessments for resistance to the disease at every step, and represents a good example of marker-assisted breeding. Commercial downy mildew resistant cvs are expected to be available in 2008–2009, some 20 years after the original identification of resistance in *A .roylei* (Scholten *et al.*, 2007).

The potentiality exists to introduce resistance to many diseases using genetic transformation (Eady, 2002). Incorporation of engineered viral protein genes into plant genomes has conferred resistance to viral disease in a number of crops. The DNA sequences that code for the coat-proteins of allium carlaviruses and potyviruses, groups that include a number of serious diseases (see Table 5.3), have been determined. Using this information it should be possible to engineer and express these sequences in alliums to induce resistance.

Many onion fungal pathogens cause damage by hyphal invasion, and this can be combated by various resistance genes. A number of these have been identified and shown to act by preventing the growth of fungal cell walls,

inhibiting the plant-damaging enzymes produced by invading fungi or by detoxifying fungal toxins. An example of the latter type is the gene encoding the enzyme oxalic oxidase, which produces an enzyme that breaks down the fungal toxin oxalic acid to carbon dioxide and hydrogen peroxide. This stops oxalic acid decreasing tissue pH which, in turn, prevents the fungal pathogenic enzymes from working effectively. This gene has been introduced into other plant species and found to inhibit fungal invasion. It has now been introduced into onions using *Agrobacterium*-mediated transformation (Eady *et al.*, 2005). Oxalic acid is the toxin produced by *Sclerotium cepivorum*, the causal agent of onion white rot, when it invades roots. Another intriguing possibility for preventing this intractable disease is to use 'gene silencing' techniques to 'switch off' the genes responsible for producing the volatile sulfur compounds in allium roots. *Sclerotium cepivorum* sclerotia are stimulated to germinate by the release of these substances in soil. A root-specific alliinase enzyme has been identified and, by 'silencing' the gene coding for this enzyme, the release of the sulfur compound germination signal to the disease fungus might be prevented, thereby avoiding infection (Eady, 2002).

An interesting example of durable resistance to a pest is provided by that of onion to *Thrips tabaci*, the onion thrip, probably the most severe pest of the crop worldwide. Resistance was found in a cultivar with a wide angle of divergence of the innermost leaves, and in which successive leaf sheaths elongate beyond the older ones that enclose them. The pest normally shelters and proliferates in the crevice between the youngest leaves, so this morphological adaptation denies the pest its usual habitat. Another external change, 'glossy foliage' – caused by a lack of wax on the outside of the leaf – confers thrips resistance. This is caused by a single recessive gene allele. However, plants with this characteristic have increased susceptibility to downy mildew and purple blotch disease.

This illustrates another general problem in developing resistance. Sometimes the properties conferring resistance may increase susceptibility to other pests or pathogens, as in the last example, and sometimes they may conflict with other requirements for the crop. For example, studies on resistance to attack by the onion fly indicated that onion varieties containing high concentrations of volatile sulfur compounds were most susceptible to attack (Soni and Ellis, 1990). The fly locates onions by these compounds. However, these compounds are those that confer the flavour and pungency to onions, so a conflict between pest resistance and a requirement for a strongly flavoured onion can be foreseen.

Transgenic shallot and garlic plants have been engineered to be resistant to the beet army worm *Spodoptera exigua*, an important tropical pest. The resistant plants contain a protein toxic to the pest that is coded by a gene derived from *Bacillus thuringiensis*. This gene has been incorporated into the allium chromosomes using the *Agrobacterium*-mediated genetic transformation of callus tissue cultures of shallot and garlic. Normal plants containing the novel protein have resulted and been shown to be resistant to the pest (see Fig. 3.7b; Zheng *et al.*, 2004, 2005).

Several laboratory techniques have been developed to challenge breeding lines with a disease or pest organism, and to measure the degree of susceptibility or resistance. For example, Currah and Maude (1984) tested resistance to leaf rot caused by *B. squamosa* by giving a standard dose of *B. squamosa* to small discs of leaf on damp wadding. The discs were then incubated at a constant 15°C at 100% RH. The average time for threads of fungus mycelium to appear on the leaf disc surface was determined. There were significant differences between cultivars in the time for infection to develop. Using such 'screening tests' it is possible to test for resistance in a standard way in many lines. Resistant lines exposed by these rapid tests can then be included in larger scale and more time-consuming tests for improved resistance in field conditions. Screening tests have been reported for onion white rot, pink root disease, neck rot, onion fly and others (see relevant chapters in Rabinowitch and Brewster, 1990b).

Much of the resistance to pests and diseases has been derived by mass selection under the pressure of attack by these organisms. This still remains an important breeding strategy, and field resistance is the ultimate test for resistance developed by more sophisticated means. The landraces of cultivated alliums that have been developed in the face of the worldwide diversity of pests and diseases are probably the most important reservoir of resistance genes. Therefore, as discussed in Chapter 1, it is vital for future resistance breeding that these old varieties are conserved (Astley, 1990).

CONCLUSIONS

The breeding of edible alliums has been relatively unsophisticated compared with many important crops, because of a comparative lack of fundamental genetic and molecular genetic information. This is now changing, and particularly in the area of disease resistance – for example, in the transfer of downy resistance from *A. roylei*, new techniques are enabling the commercial development of resistant cvs (Kik, 2002).

Genetic transformation has already produced herbicide- and insect pest-resistant alliums, the use of which could reduce the need for pesticides and simplify crop management. However, despite the environmental benefits from the use of less and safer pesticides and the unlikelihood of any risks from transgenic alliums (Eady, 2002), there remains some hostility to transgenic crops, and this has prevented their commercialization in many countries. The development of hybrid cultivars seems to have been the dominant trend in onion breeding for the last 50 years, first in the USA and then in Europe and Japan. Despite this, Dowker and Gordon (1983) pointed out that there were little published data showing that hybrid cultivars are higher yielding, more uniform or of better quality than the best open-pollinated cultivars.

A comparison of hybrid and open-pollinated (OP) short- and intermediate-day cvs in New Mexico, USA found that the OP cvs performed better than the

hybrids for marketable quality, disease (pink root) resistance and yield, the latter mainly because the hybrids produced more bolters (Cramer, 2001). However, this difference may simply reflect the importance of selection for local adaptation with onions, since many of the OP varieties tested derived from a long-standing programme of breeding OP cvs at New Mexico State University, and the hybrids were from California-based breeders.

Part of the attraction of hybrid cultivars lies in the control that the breeder and seed producer maintains over them: they cannot be reproduced from farmer-saved seed, so the work invested in their development cannot be pirated. On the other hand, low and erratic seed yields have sometimes made hybrid cultivars unavailable and seeds of hybrids are two or three times the price of OPs (Cramer, 2001). Also, hybrids take a long time to develop and need sophisticated breeding and seed production facilities. The genetic base of hybrid cultivars is narrow and they contain less genetic variability than open-pollinated cultivars, so they may be less adaptable in abnormal, stressed conditions (Pike, 1986).

For all of these reasons they are not necessarily the best route to crop improvement, particularly in some of the poorer, tropical countries where there is great need for onion improvement. In these countries, as well as in wealthier temperate regions, old, open-pollinated varieties are being replaced by newer ones, often hybrids, from transnational seed companies (Currah and Proctor, 1990). The old varieties were often perpetuated by farmer-saved seed. The same trends have been noted for Japanese bunching onion varieties in Japan and for leeks in Europe (de Clercq and van Bockstaele, 2002).

As pointed out previously, it is important that the genetic diversity represented by the traditional varieties is conserved and not lost. These tendencies in allium crop breeding are typical of the situation in many crops. There is an interesting and ongoing debate centred on whether the commercial interests directing crop breeding correspond with long term public interests, particularly those of the poorer fraction of the world's population (Mooney, 1979). Partly as a result of this debate, various publicly and charitably funded agencies are involved in the genetic conservation of allium crops coordinated by the International Board for Plant Genetic Resources (Astley, 1990). It is apparent, then, that many possibilities and conflicts arising from the new biotechnologies, the globalization of breeding and seed production companies and the geopolitical debate on the conservation and use of genetic resources are well illustrated by trends in allium breeding and seed marketing.

4

Physiology of Crop Growth, Development and Yield

This chapter starts with an outline of the principles determining crop yields and how they apply to onions. This gives a context within which to discuss how environmental and internal factors control successive phases of development from seed, through shoot growth, to the harvested bulbs or shoots. Inflorescence initiation and development and seed formation are then considered, along with interrelationships between vegetative and floral growth. Models based on physiological relationships that predict crop growth, development and yield are then discussed. Onion, the most intensively studied crop, is considered primarily, followed by sections on each of the other edible alliums, which behave similarly to onion in many ways.

The physiology of bulbing and crop yield in onion was reviewed by Brewster (1990a, 1997a, b) and Bosch-Serra and Currah (2002), and research on flowering in onion has been reviewed by Rabinowitch (1990a) and Brewster (1987, 1997a, b), pollination by Currah (1990) and seed development by Rabinowitch (1990b), where more references to the research literature can be found.

FUNDAMENTAL DETERMINANTS OF YIELD

The target of vegetable allium production is a high yield of high-quality produce. The attainment of such a crop is the end result of many processes of growth and development. Well-established principles determine the yield of all crops, and some of these have been investigated for onions and leeks. The yield of a crop is determined by: (i) the quantity of light absorbed by its leaves while harvestable dry matter is being produced; (ii) the efficiency with which the absorbed light is converted by photosynthesis into sucrose; (iii) the conversion coefficient between photosynthetic sucrose and the biochemical constituents of the harvested material; (iv) the proportion of photosynthetic output transferred to the harvested fraction of the plant; and (v) the weight losses due to respiration and decay after the above photosynthetic and biosynthetic

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processes have occurred. Each of these aspects will now be considered in more detail.

The quantity of light absorbed (i) depends on the quantity of light radiating on the field, the percentage absorbed by the leaves and on the duration of growth of the yield-bearing components. Clearly then, a high-yielding crop must produce a leaf canopy with a high percentage absorption of incident light during a season of high solar irradiation. Furthermore, the longer the duration over which such a leaf canopy is transferring photosynthate to harvestable material, the higher the yield. Much of this chapter is concerned with explaining how the season of, and magnitude of, leaf canopy development is controlled by physiological responses to environmental conditions. For the bulb-forming species the situation is complex, because bulb development ultimately leads to a cessation of foliage leaf production and this prevents the renewal and maintenance of the crop leaf canopy. There is no such finite limit to the crop leaf canopy for non-bulbing species like leek and Japanese bunching onion. Nevertheless, the growth of allium crops can also be curtailed by the onset of unfavourable weather conditions or by flower stalk development (bolting).

The proportion of the total incident light intercepted by leaves depends on the area of leaf surface per unit area of ground, the Leaf Area Index (LAI). Figure 4.1 shows the relationship between LAI and percentage incident solar radiation intercepted by the leaf canopy (I%) for onions in summer in central England. This is well summarized by the equation:

$$I\% = 85.4(1 - e^{-0.377.LAI}) \qquad \text{(Eqn 4.1)}$$

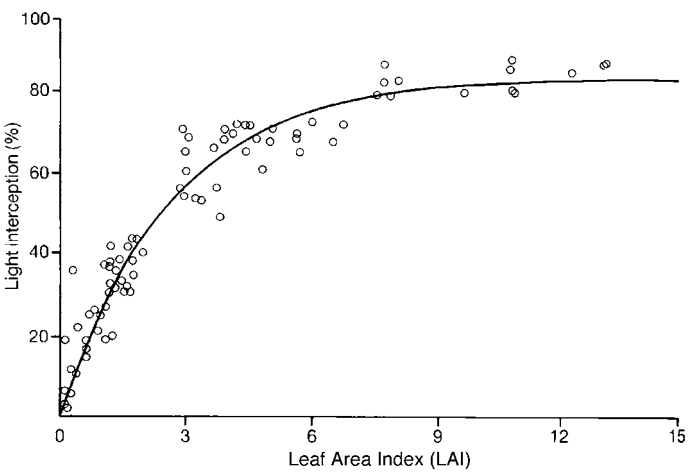

Fig. 4.1. The relationship between percentage light (photosynthetically active radiation, PAR) interception by leaf canopies of onion cv. 'Robusta' and Leaf Area Index (LAI) determined non-destructively from leaf surface areas calculated as leaf length x maximum width x 2.2 (from Mondal, 1985).

Using this equation we can calculate the LAI needed to achieve a high light interception. For example, 60% interception requires an LAI of 3.2.

The edible alliums have narrow, upright leaves, termed 'erectophile' foliage, resulting in a relatively low proportion of incident light interception per unit of leaf area compared with crops with broader, more horizontal leaves, particularly when the sun is high in the sky (i.e. at a large solar angle). Interception of photosynthetically active radiation (PAR) by crop leaf canopies frequently conforms to the equation:

$$\ln(T/I) = -k.LAI \text{ or, equivalently, } T/I = e^{-k.LAI} \qquad \text{(Eqn 4.2)}$$

T = PAR transmitted through the leaves, I = PAR incident on the crop and k is a constant, termed the extinction coefficient.

Several authors have measured k values for onions, yielding values ranging from 0.25 (Daymond *et al.*, 1997), 0.34 for the data in Fig. 4.1 for LAIs up to 4 and, assuming the ratio of extinction coefficients of PAR to that for total solar radiation is 1.21 to 0.47 (Tei *et al.*, 1996). In the latter study the values of k for lettuce and red-beet were 0.66 and 0.68, respectively. The values for onion are in the range typical of crops with leaves at a steep angle to the horizontal (Squire, 1990).

A small fraction of the intercepted PAR is reflected or transmitted, and not absorbed. Tei *et al.* (1996) found that the PAR absorbed by an onion crop averaged about 93% of the PAR intercepted after allowing for PAR reflected and PAR reflected from the ground and then absorbed. The erectophile leaf habit results in a high proportion of the leaf surface being directly sunlit compared with crops having more horizontal leaves. This promotes efficient utilization of the incident PAR when the crop is large with high LAI, but spaced seedlings capture only a small fraction of the incident PAR and are easily suppressed by light competition from overgrowing weeds with more horizontal leaves. As the onion leaf canopy grows there is a tendency for the larger leaves to fold under their own weight, resulting in the leaves becoming more horizontal in the later stages of growth (Tei *et al.*, 1996).

The efficiency with which absorbed light is converted to primary photosynthetic products (ii) can be affected by the temperature and water status of the leaves. Clearly, if temperatures are above or below the optimum for photosynthesis, efficiency will be reduced. Similarly, if leaves are water-stressed to the extent that stomata are closed and the diffusive resistance to CO_2 entry is increased, then this too will reduce photosynthetic efficiency. Therefore, for photosynthesis and growth the crop must have adequate supplies of water and mineral nutrients, and temperatures must be suitable.

The conversion coefficient between the weight of sucrose produced by photosynthesis and the weight of dry matter stored in the structural and storage tissues of the plant (iii) depends primarily on biochemical composition. A lower weight of lipid, protein or lignin is produced per unit of sucrose utilized in biosynthesis than is the case for structural or storage carbohydrates (Penning de

Vries *et al.*, 1974). The edible parts of alliums contain primarily simple sugars and fructan storage carbohydrates (see Chapter 8), plus the structural carbohydrates and protoplasmic constituents typical of most plant cells. They comprise, therefore, carbohydrate-rich tissues and should have a high ratio of final dry weight to photosynthate utilized.

As regards (iv), the extent of partition to harvestable material, in bulb onions at the optimum time for harvesting, when 80% of plants have 'soft necks', about 80% of the shoot weight is in the bulb. Bulb weight will continue to increase after this stage and the percentage of total weight in the bulbs will increase. For example, 2 weeks after the 80% 'soft necks' stage, an average of 89% of shoot dry weight comprised bulb in one series of experiments (Brewster *et al.*, 1986). Bulb onions therefore have a high 'harvest index' (the proportion of total yield in harvested material). In non-bulbing alliums the harvest index will vary according to how much green leaf is harvested in addition to the pseudostems.

In salad onions and chives nearly 100% of the shoot may be harvested. The fraction of the leek crop that is harvested varies with marketing traditions and demands. For example, in southern England the market requires the pseudostem only, whereas in northern UK leeks are sold with an additional 'flag' of green leaf above the pseudostem. Trimmed leek pseudostems comprise 33–50% of the total shoot weight, with a mean of about 40%. Leeks trimmed with a green 'flag' would typically comprise 55–60% of the total shoot weight. Clearly, the harvest index of leek crops is lower than for bulb onions.

Concerning crop respiration and decay (v), even in the absence of bolting and in favourable weather conditions, leeks can reach a maximum or 'ceiling' yield (e.g. Fig. 4.50). Theoretically, such a ceiling will be reached when dry matter gains from photosynthesis are equalled by dry matter losses due to respiration and tissue senescence. Such a situation has not been observed in onion crops, because bulb ripening and leaf senescence terminate crop development before a ceiling is reached (see Fig. 4.2).

Respiration results from two broad components – first, 'growth respiration', the CO_2 output associated with the synthesis of new tissue and, secondly, 'maintenance respiration', the CO_2 output needed to maintain existing tissues alive (McCree, 1970). The ratio of growth respiration to dry matter growth determines the photosynthate conversion efficiency (iii above) and varies with the biochemical make-up of the new growth, as indicated. Maintenance respiration varies with tissue and temperature. Leafy shoots have a much higher maintenance respiration than storage organs like bulbs (de Visser, 1994a; Tei *et al.*, 1996). Onion and garlic bulbs in store have very low respiration rates (see Chapter 7, 'Bulb Respiration Rates').

Onion bulbs taken directly from plants still actively growing in the field had maintenance respiration rates of 0.0010 and 0.0011 g CO_2/g/day at 9 and 19°C, respectively – about 58% the rate of red-beet storage roots in the same conditions and less than 5% of the maintenance respiration rates typical of leaves and stems (Tei *et al.*, 1996). Respiration rates per unit of crop dry weight

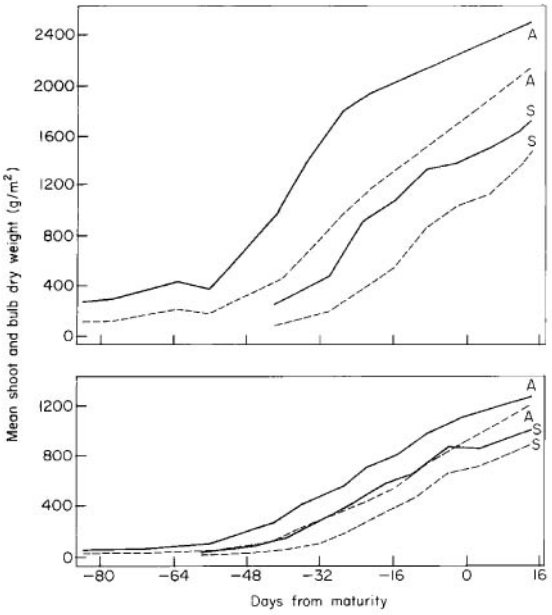

Fig. 4.2. The change of total shoot (solid lines) and bulb (broken lines) dry weight with time of irrigated, well-fertilized onion crops when grown at 400 (upper graph) and 50 plants/m^2 (lower graph). A, autumn-sown, S, spring-sown (from Brewster *et al.*, 1986. Courtesy of *Annals of Botany*).

will be low as harvest approaches in onions, since they have a large proportion of the total weight in the bulb (see (iv) above). The overall maintenance respiration rate of bulb onions close to the normal harvest time (i.e. with 81% of the shoot dry in bulbs) was estimated as 0.0035 g CO_2/g dry matter/day, only 60% of the value of a beet crop at a comparable stage (Tei *et al.*, 1996).

The net result of these processes, total dry biomass production, has been investigated in onions. Well-irrigated onion crops produce, during bulbing, an average of about 1.6 g of shoot dry matter per MJ of solar radiation intercepted by the leaf canopy. Similar conversion efficiencies have been reported for potatoes, sugarbeet and in cereals before anthesis. However, values of mean conversion efficiency vary, and are low in conditions of high irradiance (high light levels) and high temperature, and high in lower-irradiance, lower-temperature conditions (Brewster *et al.*, 1986).

As might be expected, lack of irrigation in dry weather decreases conversion efficiency. In well-irrigated crops a range of conversion factors between 1.2 and 2.0 g/MJ has been observed. Tei *et al.* (1996) reported an efficiency of conversion of absorbed PAR to dry-matter of 5.08 g/MJ in a well-irrigated and -fertilized bulb onion crop during the bulbing phase. Efficiencies of red-beet and lettuce in the same experiment were 71 and 48% of the onion value, respectively.

About 50% of total solar radiation energy is PAR (Squire, 1990), so these efficiencies in terms of PAR should be halved for comparison with results based on total solar irradiance.

AGRONOMIC FACTORS INFLUENCING BULB ONION YIELDS

In a study comparing well-irrigated autumn- and spring-sown bulb onion crops, yields varied by a factor of more than five depending on cultivar, sowing date and plant density (Mondal, 1985). Such large differences in yield cannot be explained solely by differences in the efficiency with which intercepted light is converted into dry matter. In Table 4.1 we see that bulb yield increases with plant density and that this correlates with the percentage light interception by the crop leaf canopy. Table 4.2 shows how yields are reduced by delaying sowing. Later-sown plants switched from leaf blade to bulb production while the Leaf Area Index (LAI) and, consequently the leaf canopy light interception, was lower than for earlier-sown plants. A similar effect, but this time caused by a difference in maturity date between cultivars sown at the same time, is illustrated in Table 4.3. The later-maturing cultivar had longer to develop a high LAI before the switch to bulb growth. From Tables 4.1, 4.2 and 4.3 it is clear that a high bulb yield is dependent on a high percentage of light interception by the leaf canopy (see Fig. 4.3). This requires sufficient time in conditions conducive to leaf blade growth before bulbing starts.

Although important, percentage light interception was not the only factor involved since, in these experiments, autumn-sown onions produced a higher yield than spring-sown at a given percentage interception (see Fig. 4.3). For crops with 60% light interception the duration of bulbing was 55 days when autumn-sown and 43 days when spring-sown, and consequently the former intercepted more light in total during bulbing.

Longer duration of bulbing may be caused by cooler temperatures, giving slower bulb ripening and leaf senescence. Mean temperatures during bulbing

Table 4.1. The effect of planting density on bulb yield and light interception for onion cv. 'Augusta' sown on 21 April 1982 at Wellesbourne, UK.

	Planting density (plants/m^2)		
Effect	25	100	400
Bulb yield (kg/m^2 of dry matter)	0.46	0.71	1.02
Leaf Area Index (LAI) during bulbing	0.82	1.5	2.3
Percentage light interception by leaf canopy during bulbing	30.0	46.0	59.4
Maturity date	14 Aug	2 Aug	24 July

Table 4.2. The effect of sowing date on bulb yield and light interception for onion cv. 'Augusta' at Wellesbourne, UK; means of plots with 400, 100 and 25 plants/m^2.

	Sowing date	
Effect	15 March	21 April
Bulb yield (kg/m^2 of dry matter)	1.04	0.73
Leaf Area Index (LAI) during bulbing	3.7	1.5
Percentage light interception by leaf canopy during bulbing	69	45

Table 4.3. A comparison of bulb yield and light interception by early-maturing and later-maturing (maincrop) onions grown at a density of 100 plants/m^2 and sown on 21 April at Wellesbourne, UK.

	Cultivar	
	'Augusta'	'Robusta'
Bulb yield (kg/m^2 of dry matter)	0.71	0.99
Leaf Area Index (LAI) during bulbing	1.5	2.8
Percentage light interception by leaf canopy during bulbing	46	66
Maturity date	25 July	12 August

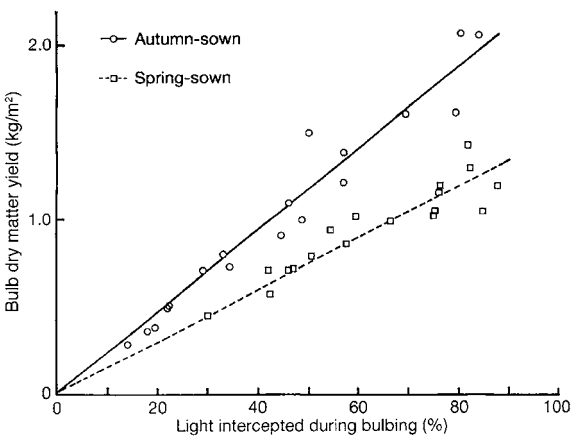

Fig. 4.3. The relationship between percentage light (PAR) interception by the leaves during bulbing and bulb dry matter yield for well-fertilized and -irrigated onion crops at Wellesbourne, UK.

were 13°C for the autumn-sown crops and 17.5°C for the spring-sown. Direct evidence for this comes from experiments where onion cv. 'Hysam', which is very similar to cv. 'Robusta' of Table 4.3, was grown along a gradient of temperatures. Bulb yields approximately halved with an increase in mean temperature from 12 to 19°C (Daymond *et al.*, 1997). This decrease in yield corresponded with a decrease in the interval between onset of bulbing and maturity from about 117 to 55 days (see Fig. 4.4). LAI at the start of bulbing, and therefore light interception, did not differ over the temperature range. Therefore, the decrease in bulb yield at warmer temperature can be attributed to a shorter duration of bulb growth, causing less PAR to be converted into bulb dry matter.

When the atmospheric CO_2 concentration was increased from 374 to 532 μmol/mol there was a large yield increase at all temperatures, but little effect on the rate of crop development (see Fig. 4.4a). These results indicated that the yield increase caused by this rise in atmospheric CO_2 would more than compensate for the lower bulb yield resulting from the temperature increase predicted for the 'global warming' effect of such a CO_2 increase. Under UK conditions it appears that elevated atmospheric CO_2 and the consequent global warming would benefit bulb onion production.

As Table 4.1 shows, leaf canopy light interception may be increased by growing at higher plant densities but, although yields increase, individual bulb size is drastically reduced, and this is not normally acceptable. Most markets require bulbs of 5–7 cm diameter and in fertile conditions this dictates a plant density in the range 50–100 plants/m^2 (see Fig. 6.8). Therefore, to achieve a high yield of medium to large bulbs, a cultivar with the capability of producing sufficient leaf area to intercept a high proportion (> 60%) of the incident light must be sown at the appropriate time.

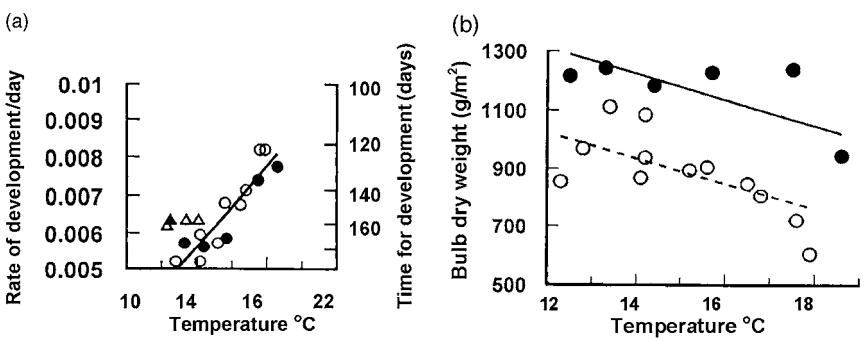

Fig. 4.4. (a) The relationship between the rate of crop development from transplanting to maturity and mean temperature for onion cv. 'Hysam' grown at elevated (●, ▲) and normal (○, △) CO_2 (532 and 374 μmol/mol CO_2, respectively). (b) The relationship between bulb dry matter yield at harvest and mean temperature from transplanting to harvest maturity at elevated (●) and normal (○) CO_2 for onion cv. 'Hysam' (a) from Fig. 1 and (b) from Fig. 4 of Daymond *et al.*, 1997. Courtesy of *Journal of Horticultural Science*).

SEED VIABILITY, GERMINATION AND EMERGENCE

The first stage in the production of a good onion crop is to sow viable seed at an appropriate density and achieve a high level and uniformity of seed germination and seedling emergence. Many of the processes fundamental to this aim have been studied in onions and many of the principles established apply to other crops, particularly the small-seeded vegetable crops.

Seed storage and viability

The viability of onion seeds can decline rapidly if they are stored in warm, moist conditions, a feature common to most orthodox seeds (Ellis, 1991), and which presents difficulties for maintaining seed quality in tropical areas. Orthodox seeds, like the alliums and most crop species, can tolerate desiccation, and storage longevity is increased thereby. At sufficiently low moisture contents such seeds can tolerate sub-zero temperatures and this can further increase longevity. In view of the importance of the long-term storage of viable seeds for genetic conservation (Astley, 1990), equations for predicting the effects of storage conditions on the loss of seed viability have been developed and applied to onions among other crops (Ellis and Roberts, 1980a, 1981; Ellis, 1991).

If the percentage of seeds that germinate is plotted against time of storage in constant, controlled conditions, a sigmoidal curve that conforms to a negative cumulative normal distribution results (Ellis, 1991; Fig. 4.5a). This implies that different seeds die at different times and that the frequency distribution of seed deaths is normal. If the percentage germination scale is transformed to a probability scale known as probits, where percentage germination is in units of standard deviation of the distribution of seed longevity, the relation between percentage germination and time becomes linear (see Fig. 4.5b).

The standard deviation of the frequency distribution of seed death in time is also a time and hence a period of longevity and, from the properties of the normal distribution, it represents the time taken for longevity to fall from 97.7 to 84.1% or from 84.1 to 50%. The straight line relationship between probit percentage viability and time can be represented as:

$$V = K_i - p/\nu \qquad \text{(Eqn 4.3)}$$

where
V = probit percentage viability
p = days in storage
ν = the standard deviation of the distribution of time until seed death in the storage environment
K_i = a constant for the seed-lot representing the initial viability of the seed-lot at the start of storage.

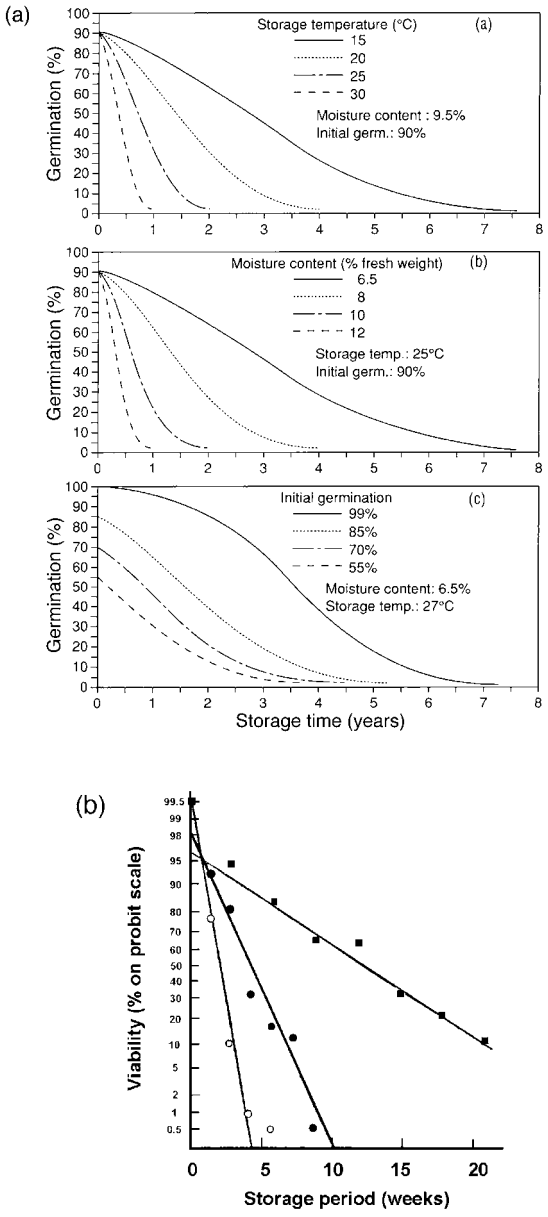

Fig. 4.5. Environmental effects on stored onion seeds. (a) The influence of temperature, seed moisture content and initial viability on onion seed survival. The ageing curves were developed using Eqn 4.3 (Taylor, 1997. Courtesy of CABI, Wallingford, UK). (b) Survival curves of onion seed of 18% moisture content at 25 (■), 30 (●) and 35°C (○). Percentage viability is plotted on a probability scale (redrawn from Ellis and Roberts, 1977).

Above 3.5% of seed moisture, the standard deviation, ν, i.e. longevity, declines as seed moisture content increases, such that the log ν declines linearly with increase in log moisture content (see Fig. 4.6). Below 3.5% moisture content there is no further increase in longevity with drying (see Fig. 4.6). Storage at or below this moisture content, known as 'ultra-dry' seed storage, results in maximal longevity (Ellis *et al.*, 1996). At 3.5% moisture content the onion seeds are in equilibrium, with a relative humidity of 10% in the surrounding atmosphere equivalent to a water potential of –311 Pa, a value around which many crop seeds reach their maximum longevity and which corresponds to the remaining water in the seeds being in a strongly bound state (Ellis *et al.*, 1990).

Seed longevity decreases at an accelerating rate as temperature increases. Over the range −20 to 90°C a wide range of species show the same relationship, with $\log_{10}\nu$ (i.e. longevity) decreasing as a quadratic function of temperature. Effects of moisture content and temperature on longevity of onion seeds have been quantified by Equation 4.4 (Ellis and Roberts, 1980a):

$$\underset{K_E}{\mathrm{Log}_{10}\nu = 6.975} - \underset{C_w}{3.470\log_{10}m} - \underset{C_H}{0.04T} - \underset{C_Q}{0.000428T^2} \qquad \text{(Eqn 4.4)}$$

where
ν = standard deviation of the distribution of seed longevity (days)
m = seed moisture content as a percentage of moist weight
T = temperature °C.

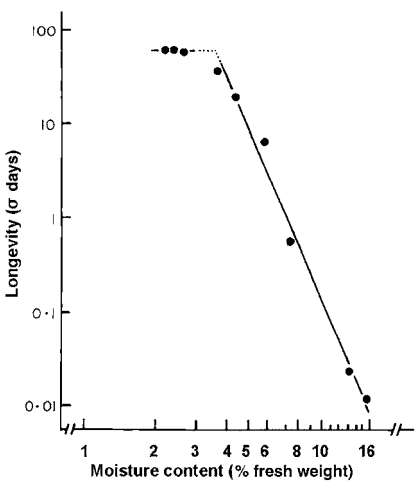

Fig. 4.6. The relation between seed moisture content of onion seeds, shown as the percentage of fresh weight on a logarithmic scale, and the standard deviation of seed deaths in time, σ (a measure of seed longevity expressed as days on a logarithmic scale), after hermetic storage at 65°C. The critical moisture content is where the lines intersect (from Ellis *et al.*, 1990. Courtesy of *Annals of Botany*).

This relationship has been combined with Eqn 4.3 to give an equation that that predicts the percentage germinable (i.e. viable) seeds in a seed-lot after storage at known moisture content, m and at temperature T (Ellis and Roberts, 1980a):

$$V = K_i - p/\ 10^{(6.975 - 3.470\log_{10} m - 0.04T - 0.000428T.T)} \qquad \text{(Eqn 4.5)}$$

where
V = probit percentage of germinable seeds
K_i = seed-lot constant
p = period of storage, days
m and T as for Eqn 4.4.

The constants 6.975 (K_E) and 3.470 (C_W) are characteristic of the species, i.e. onion. The constants 0.04 (C_H) and 0.000428 (C_Q) have been found similar for all species investigated (Ellis, 1991). K_i, the seed-lot constant, varies depending on the seeds' environment before entering controlled storage. K_i is the probit percentage viability at the beginning of storage; it is best estimated by an initial rapid ageing test of the seeds, which involves keeping them moist at warm temperatures and measuring their decline in viability. Simple estimates of initial percentage viability from germination tests are subject to large sampling errors, and small differences have a large effect on K_i (Ellis and Roberts, 1980b).

Germination and seedling emergence

The fact that seeds emerge more quickly from moist, warm soil rather than from cold, dry soils must have been known to the earliest agriculturalists. However, it is only relatively recently that scientists have developed a quantitative understanding of the relationships between soil temperature and moisture and the germination and emergence of seedlings. The effects of soil strength (mechanical impedance) on emergence and germination are also beginning to be understood quantitatively. Onions and leeks have frequently been used in the studies, and their responses typify patterns common to most crop species while having quantitative responses particular to them. These can be compared and contrasted with other crops and they point to particularities of response that can give useful insights for establishing these crops in the field.

Two aspects of germination are important – first, the percentage of seed to germinate and, secondly, the rate of germination. The rate of germination can be quantified as the reciprocal of the time for a certain percentage, usually 50%, of the total number of seeds to germinate (Hegarty, 1972). Figure 4.7 shows the response of both rate and percentage germination of onion seeds to temperature in the absence of moisture stress. Above 25°C both rate and percentage germination decline, but between 5 and 25°C the rate of germination increases almost linearly.

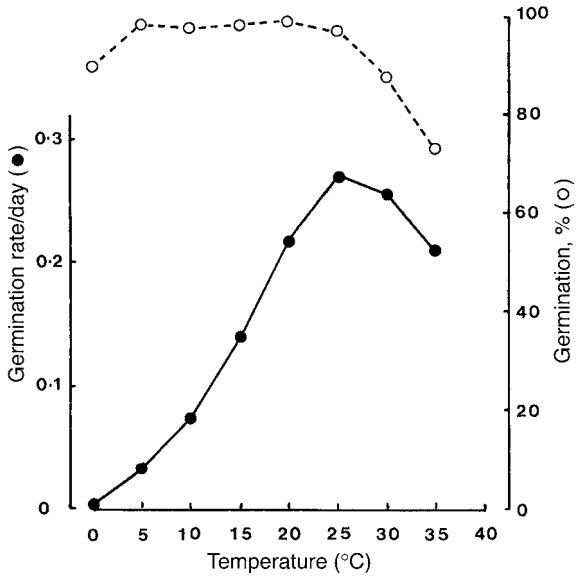

Fig. 4.7. The relationship between temperature and the rate and percentage germination of onion seeds on moist paper. Rates were calculated as reciprocals of the number of days for 50% of the viable seeds to germinate (from Harrington, 1962).

In Fig. 4.7 the rate of germination in the range 5–25°C is approximated by a straight line equation:

$$\text{Germination rate} = 1/t = b(T - T_b) \qquad \text{(Eqn 4.6)}$$

where
t = time to 50% germination, days
T = temperature ($5 < T < 25$°C)
T_b = base temperature, where the fitted line projects to zero rate – for these data 2.5°C
The 'thermal time' or 'heat sum' required for 50% germination, Θ, is given by:

$$\Theta = (T - T_b)t \qquad \text{(Eqn 4.7)}$$

The 'thermal time' or 'heat sum' required for 50% germination combines the effect of time and temperature on germination and quantifies the fact that a warm day is more effective than a cool day in progressing germination. In the case of Fig. 4.7, 80°C days above a base temperature of 2.5°C are required for 50% germination. The units °C days are variously know as 'day degrees', 'degree days', 'thermal time units' or 'heat units' above 2.5°C. For example, 80°C days could be achieved by 4 days at 22.5°C or 16 days at 7.5°C. In fluctuating temperatures time of emergence can be estimated by summing the heat units accumulated during the time at each temperature (Wagenvoort and

Bierhuizen, 1977), provided that temperatures remain < 25°C. Many plant developmental processes require a certain thermal time or number of heat units above an appropriate base temperature to complete, and the concept is widely used in crop technology.

The elongation of radical and shoot after germination in moist conditions depends similarly on temperature (see below), and a relationship like Eqn 4.7 predicts the emergence of onion seedlings sown in moist soil (Bierhuizen and Wagenvoort, 1974). They found that, over the range 3–17°C, 219°C days above a base temperature (T_b) of 1.4°C was required for 50% emergence of onions. This base temperature was similar to that of many temperate zone vegetables, but the heat sum ranked fourth highest out of 31 common vegetable species – only celery, parsley and leek (requiring 222°C days above a T_b of 1.7°C) had higher heat sums, and the former two species are notoriously slow to emerge because of inhibitors in the seedcoat.

These results show that onion and leek emergence is comparatively slow: onions will take 2.25 times as long as turnips to reach an equivalent stage of emergence after sowing in moist soil. From summing up the heat units accumulated during a time at each temperature, the same number of heat units were shown to be predictive of a 50% emergence of onions from soil in fluctuating temperatures in the range 3–21°C (Wagenvoort and Bierhuizen, 1977).

The above analysis ignores the fact that different seeds germinate and emerge at different rates and that there is a considerable spread in time for these events. Various proposals have been suggested for quantifying these rates for different percentiles of the seed population. If, as is often the case (see Fig. 4.8a), percentage germination follows an S-shaped curve, then this often conforms to a cumulative normal or log-normal distribution (Covell *et al.*, 1986). Moreover, it is frequently the case that, although different percentiles (G) of the population germinate at different rates, they do not have significantly different base temperatures, T_b. They therefore differ only in the thermal time, $\Theta(G)$ above T_b for germination to occur, and $\Theta(G)$ values conform to a normal or log-normal distribution. Such distributions can be characterized by two constants, K and ν, where ν is the standard deviation of the frequency distribution of thermal time to germination in the seed population and K is an intercept constant at thermal time zero; these constants can be estimated using probit analysis (Covell *et al.*, 1986). Figure 4.8a shows the response of cumulative germination of onions cv. 'White Lisbon' to thermal time at suboptimal temperatures (10–25°C).

As seed ages and the percentage of all viable seeds declines, the mean time to germination of surviving seeds at near-optimal temperatures increases (see Fig. 4.9a). The thermal time to 50% germination at suboptimal temperatures also increases (see Fig. 4.9b).

Germination rate frequently rises to a fairly sharp optimum and then decreases with temperature (see Fig. 4.7) but, in other cases, there is a broader optimum range. In one study of onion germination the optimum temperature for germination was higher for the quick-germinating seeds, i.e. lower percentiles,

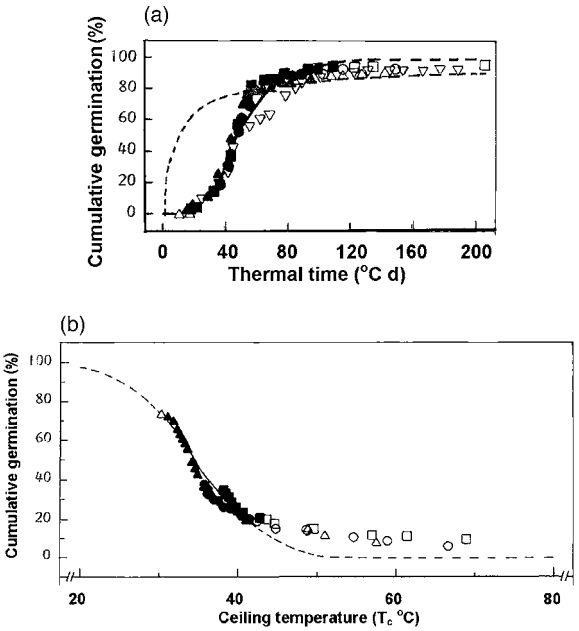

Fig. 4.8. (a) The response of cumulative germination (G, %) to thermal time at suboptimal temperatures for germination for onion seeds of cv. 'White Lisbon' from observations at 10.0 (○●), 15.0 (□■), 20.0 (△▲) and 25.5°C (▽▼). The sigmoid fitted curve was derived by fitting Eqn 4.8 to the data represented by solid symbols. The other (faster germinating) broken line shows the response for primed seed that had not been dried following priming. (b) The relation between ceiling temperature for germination and the germination percentile of onion seed cv. 'White Lisbon' from data collected at 29.7 (△▲), 34.8(○●) and 37.8°C (□■). The curve shown is the response fitted by probit analysis of the observations denoted by solid symbols and has the equation: Ceiling Temperature (°C) = (4.55-probit(G))7.58. This equation forms part of Eqn 4.9 (from Ellis and Butcher, 1988. Courtesy of *Journal of Experimental Botany*).

than for the later ones. There was not a sharp temperature optimum for the whole seed-lot; it depended on seed quality and could therefore decline as these seeds aged (Ellis and Butcher, 1988).

Above the optimum temperature, the rate of germination declines, often linearly with increasing temperature, to zero rate at the ceiling temperature for germination, T_c (Ellis *et al.*, 1986). An analysis of onion germination rates excluding the fastest 20% to germinate using a model previously found to describe germination of certain leguminous species (Ellis *et al.*, 1987) indicated that, T_c, the ceiling temperature for germination, was normally distributed and was lower for the late-germinating seeds (see Fig. 4.8b). The equations derived by Ellis and Butcher (1988) to describe the response and variation in response of onion cv. 'White Lisbon' germination rates to both sub- and supra-optimal temperatures are as follows:

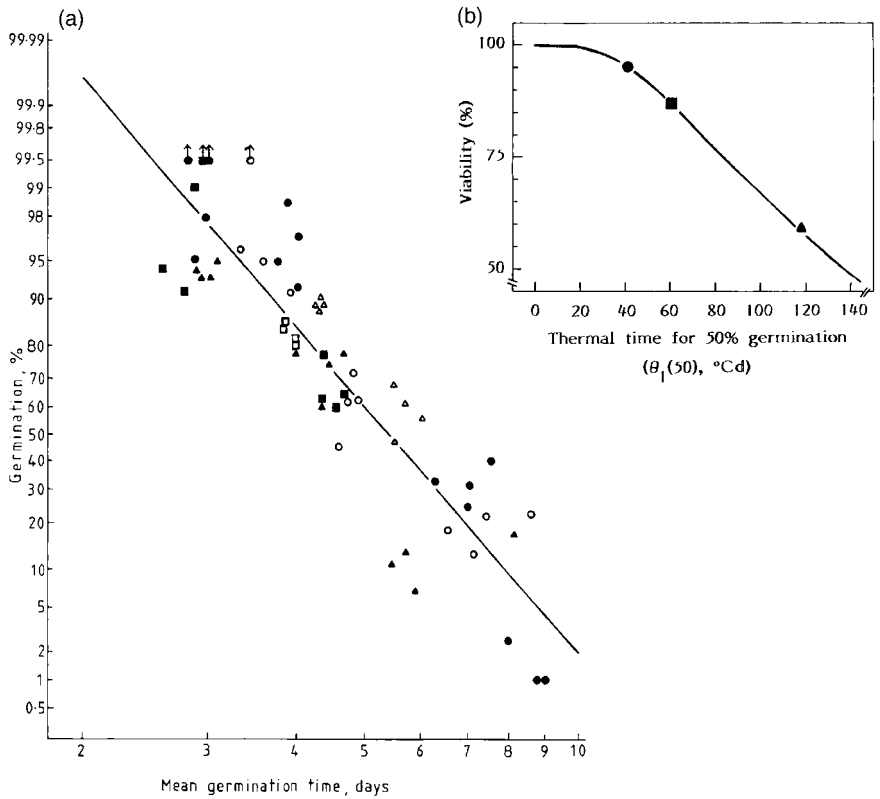

Fig. 4.9. Illustrations of the negative association between seed viability and time to germinate. (a) The relationship between the percentage germination (probability scale) and the mean germination time at 20°C (log scale) for three seed-lots of onion cv. 'White Lisbon' (solid symbols) and three of cv. 'Rijnsburger' (open symbols) before and after different periods of storage at 45°C at 18% moisture (from Ellis and Roberts, 1981. Courtesy of *Seed Science and Technology*). (b) The relation between percentage germination at 19.1°C and the thermal time needed for 50% germination at suboptimal temperatures for seed-lots of onion cv. 'Senshyu Semi-globe Yellow' produced in three different years (from Ellis and Butcher, 1988. Courtesy of *Journal of Experimental Botany*).

The equation that relates rate of germination to temperature at suboptimal temperatures for each percentile of the seed population is:

$$1/t(G) = (T-3.5)/10^{[(\text{probit}(G) + 9.134)0.1844]} \qquad \text{(Eqn 4.8)}$$

where
t(G) = time for the Gth percentile to germinate, days
T = temperature, °C

The base temperature is 3.5°C, −9134 is the K value and 0.1844 the ν value (see text above for explanation).

Probits are taken from tabulated values with probit 50% taken as 0 rather 5 as is sometimes done.

At supra-optimal temperatures the equation is:

$$1/t(G) = ([\{4.55 - \text{probit}(G)\}7.58] - T)/19.75 \qquad \text{(Eqn 4.9)}$$

T and t(G) have the same meaning as in Eqn 4.8, 4.55 is a fitted constant, 19.75°C day is the thermal time needed for germination at supra-optimal temperatures and 7.58 is the standard deviation of ceiling temperature for the seeds. The term '{4.55 − probit(G)}7.58' is the ceiling temperature for germination of the Gth percentile of the seed population.

The response of onion germination rates to temperature over middling percentiles (within the range for which the data was fitted and where probit analyses is most accurate) predicted by Eqns 4.8 and 4.9 is shown in Fig. 4.10. The graphs show that the optimum temperature for germination is higher for the lower percentiles, i.e. the fastest germinators, and that these seeds also have a higher ceiling temperature for germination, T_c, than the lower percentiles. The graphs also indicate a decreasing percentage of seeds germinating as temperature increases above about 25°C, as in Fig. 4.7, as the ceiling temperatures, T_c, for progressively lower percentiles (i.e. slower-germinating seeds) are exceeded.

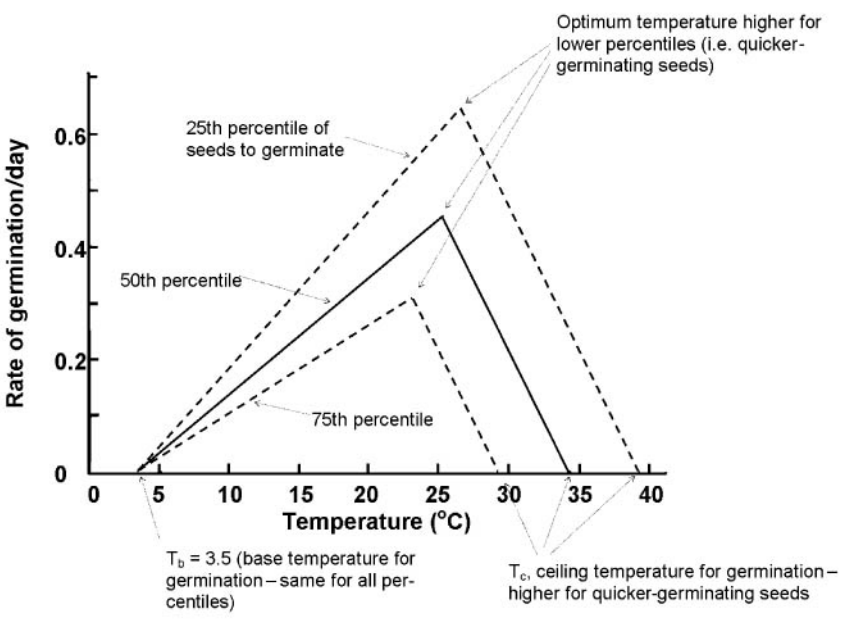

Fig. 4.10. The response of germination rate to temperature in three cohorts (percentiles) of onion seed cv. 'White Lisbon' as predicted by Eqns 4.8 and 4.9.

Effects of water stress on germination

The responses of germination and emergence to temperature described above derive from studies of seeds on moist filter paper or in moist soil. Under conditions of water stress, rates and percentages of germination decrease as stress increases (see Fig. 4.11a, b; Rowse and Finch-Savage, 2003).

Responses of germination rate to temperature and water potential have been modelled by extending the concept of thermal time for germination to hydrothermal time for germination. Here, the effectiveness of a temperature for advancing germination in the suboptimal range depends on the water potential around the seed, as defined by its level above a base water potential below which germination cannot occur (Rowse and Finch-Savage, 2003), thus:

$$\Theta_{HT} = (\psi - \psi_b(G))(T - T_b)t(G) \qquad \text{(Eqn 4.10)}$$

Θ_{HT} = hydrothermal time for germination, MPa°Cd

ψ = water potential around seed, MPa

$\psi_b(G)$ = base water potential below which the germination cannot occur for the Gth percentile of the population, MPa

T = temperature, °C

T_b = base temperature for germination, °C

t(G) = time for Gth percentile to germinate (days)

Θ_{HT} and T_b are assumed constants, while $\psi_b(G)$ varies with a percentile (G) and this determines the germination time for that percentile. If the frequency

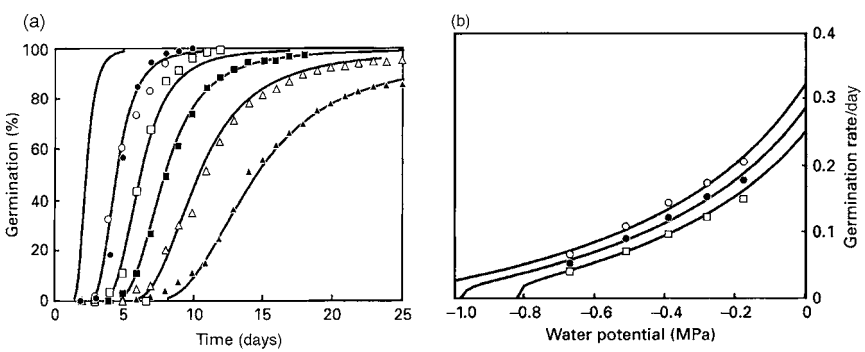

Fig. 4.11. Effects of water stress on onion seed germination. (a) Cumulative germination with time at 15°C for onion seeds subjected to water potentials of 0 (○), –0.175 (●), –0.28 (□), –0.39 (■), –0.51 (△) and –0.67 MPa (▲). Symbols are experimental data and lines are calculated from a 'virtual osmotic potential' (VOP) model. (b) Germination rates at 15°C (reciprocal of germination time) for the 20th (○), 50th (●) and 80th (□) germination percentiles of onion seeds as determined by the surrounding water potential. Lines are calculated from the VOP model (from Rowse *et al.*, 1999. Courtesy of *New Phytologist*©, 1999).

distribution of $\psi_b(G)$ is known, then the distribution of t(G) can be predicted. If the distribution of $\psi_b(G)$ is normal, defined by a standard deviation of ψ_b ($\nu_{\psi b}$), then probit analysis can be used to fit values to the constants in Eqn 4.10 using data on rates of germination in different temperatures, T and water potentials, ψ. If $\psi_b(G)$ increases with temperature, as has been found true of some species (Rowse and Finch-Savage, 2003), then increases in germination rate as a result of increased temperature are offset by the increasing $\psi_b(G)$ and germination rate rises to a maximum at an optimum temperature and then decreases, with further increase in temperature (Rowse and Finch-Savage, 2003; Finch-Savage, 2005).

An alternative to hydrothermal time models for predicting the response of germination to temperature and water potential has been developed (Rowse *et al.*, 1999; Rowse and Finch-Savage, 2003). This approach is based on the idea that, for visible germination to occur, metabolic activity in the seed must generate sufficient osmotic pressure within the cells of the radical for the turgor pressure of these cells to exceed the yield threshold, Y, of the cell walls, thereby allowing radical expansion and emergence from the seedcoat. In this model it is assumed that progress in generating osmotic potential occurs if the osmotic potential around the seeds exceeds a minimum, ψ_{min}. The value of ψ_{min} is below the minimum water potential necessary for germination, ψ_b. The fact that progress towards germination occurs at ψ levels below ψ_b in a seed priming (see Chapter 6, 'The Priming of Seeds'), means that this model includes the full range of water potentials at which seeds are physiologically active. Based on these ideas, Rowse and Finch-Savage (2003) derived Eqn 4.11 to predict the time to germination of percentile G of a seed population:

$$t(G) = 1/[k(1 - \psi / \psi_{min})(T / T_b - 1)] \ln [(\psi_b(G,T) - Y) / (\psi_b(G,T) - \psi)] \qquad \text{(Eqn 4.11)}$$

The constants and variables are defined below and the numbers in brackets following the definitions are the best fitting values for onion (Rowse and Finch-Savage, 2003):

t(G) = time for percentile G of the seed population to germinate, days

T = temperature around the seed, °C

T_b = base temperature for germination, °C (= 1.2)

ψ = water potential around the seed, MPa

$\psi_b(G,T)$ = base water potential above which the Gth percentile of the population can germinate at temperature T°C MPa (= –0.87 for $\psi_b(50)$ when T < T_d, see Eqn 4.12, below)

ψ_{min} = the minimum water potential for metabolic advancement of the seeds towards germination, MPa (= –4.18)

Y = yield threshold of radical (young root) cell walls that opposes cell expansion by turgor pressure, MPa (= 0.71)

k = rate constant relating germination rate to temperature above T_b, the base temperature when there is no water stress (i.e. when ψ = 0)/day (= 0.014)

Between the base temperature, T_b, and T_d, a temperature somewhat below the optimum for germination (see Fig. 4.12b), ψ_b is constant for a particular percentile G. Above T_d, ψ_b increases linearly with temperature with slope m (= 0.051 MPa°/C) (see Fig. 4.12b).

The above conditions are expressed as:

$$T_b < T \leqslant T_d;\ \psi_b(G,T) = \psi_b(G)_d$$
$$T_b < T \leqslant T_c;\ \psi_b(G,T) = \psi_b(G)_d + m(T - T_d) \qquad \text{(Eqn 4.12)}$$

Here, T_c is the ceiling or maximum temperature for germination of the percentile concerned.

The spread of germination for different percentiles of the population is due to variation in $\psi_b(G)$, the base water potential for germination for each percentile. In the model of Rowse and Finch-Savage (2003), the distribution of $\psi_b(G)$ is assumed normal and is characterized by the standard deviation $\nu_{\psi b}$ (MPa), the optimised value of which was 0.21MPa. Although ψ_b increases above T_d, $\nu_{\psi b}$ is assumed not to change.

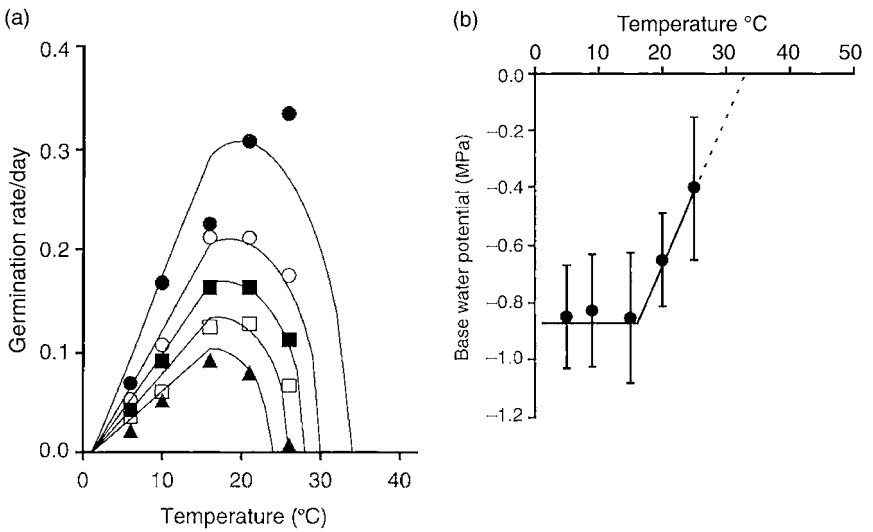

Fig. 4.12. Combined temperature and water potential effects on onion seed germination. (a) The effect of temperature and water potential on the germination rate (reciprocal of the time to 50% germination, days) of onion seeds. Water potentials 0 (●), –0.18 (○), –0.28 (■), –0.39 (□) and –0.51 MPa (▲). The lines are fitted according to Eqns 4.11 and 4.12. (b) The effect of temperature on the base water potential, $\psi_b(50)$, below which germination will not occur for the 50th percentile in onion seed germination. The values of $\psi_b(50)$ were calculated according to the 'virtual osmotic pressure' VOP model of Eqn 4.11. Vertical lines are the standard deviation of $\psi_b(50)$ (from Rowse and Finch-Savage, 2003. Courtesy of *New Phytologist*©, 2003).

The response of germination of onion cv. 'Hyton' to a range of constant water potentials and temperatures was well characterized by Eqn 4.11, with the optimized parameters given with the definition of terms under Eqns 4.11 and 4.12 (see Fig. 4.12a). Figure 4.12b shows how $\psi_b(50)$ is constant until T_d, and then increases linearly. The temperature at which $\psi_b(50)$ reaches zero is the ceiling temperature for germination for the 50th seed percentile – predicted to be 33°C – quite close to the value in Fig. 4.8b from Ellis and Butcher (1988). A hydrothermal time model (Eqn 4.10), with ψ_b increasing above a T_d of 17°C, gave similar results to Fig. 4.12a and similar values to the constants that were common to both models, namely T_b, ψ_b, $\nu_{\psi b}$, T_d and m.

Although based on the idea that germination results from osmotic potential decreases that drive turgor pressure to exceed a critical yield threshold, Y in the root cell walls, Rowse and his colleagues have termed their model the 'Virtual Osmotic Potential' (VOP) model. This is because the assumption of a constant Y is unproven, and some evidence from other species indicates that Y decreases to allow germination. Nevertheless, the equations derived from this postulate provide a model that includes the effects of temperature and water potential on both the germination rate and percentage germination. Above T_b and below T_d the germination rate increases linearly with temperature (see Fig. 4.12a). At high temperatures, the percentage germination at any water potential decreases as temperature increases above T_c, the critical or maximum for germination, for progressively lower percentiles of the population. Figure 4.12a shows that T_c decreases as ψ decreases, as does optimum temperature for germination, T_{opt}. These effects of temperature on T_{opt} and T_c are indirect, and are caused by the increase of ψ_b as temperature increases above T_d (see Fig. 4.12b). The lack of a sharp peak for germination rate at T_{opt} corresponds with some of the results of Ellis and Butcher (1988), and has been observed in a number of other species. The VOP model also allows progress towards germination at water potentials lower than ψ_b, as occurs during seed priming. Hydrothermal time models require a separate treatment for these conditions and the introduction of a further concept of 'hydrothermal priming time' for water potentials between ψ_{min} and ψ_b.

The VOP model can be formulated to sum progress towards germination in the varying temperatures and water potentials that occur under field conditions. Increases in the virtual osmotic pressure, $\psi_{\pi v}$, in the seed for successive steps in time at varying temperature, T and water potential, ψ can be summed until ψ_b is exceeded and germination is predicted to occur. Eqn 4.13 is the appropriate formulation (Rowse and Finch-Savage, 2003), and this is now used in computer simulations of field emergence of onion seedlings (Rowse and Finch-Savage, 2005):

$$d\,\psi_{\pi v}(G)/dt = k(1 - \psi / \psi_{min})(T / T_b - 1)[\psi_b(G) - Y - \psi_{\pi v}(G)] \qquad \text{(Eqn 4.13)}$$

with symbols as defined above for Eqn 4.11 for ψ_b constrained as in Eqn 4.12.

Temperature and soil moisture effects on field germination and emergence

A simplified model based on hydrothermal time concepts (Eqn 4.10) has given good predictions of onion emergence from field sowings (Finch-Savage and Phelps, 1993) and indicates the optimum timing of a single irrigation after sowing to maximize the percentage seedling emergence and minimize the spread of emergence (Finch-Savage, 1990; Finch-Savage and Steckel, 1994). It is assumed that germination, i.e. the emergence of the radicle from the seedcoat, is the most moisture-sensitive stage in germination and emergence. For the radical to appear, the water potential around the seed must exceed a critical threshold, ψ_b, which is about –1.1 MPa for onions (Finch-Savage and Phelps, 1993). Therefore, the water potential ψ_b is a critical barrier restricting seedling development until it is exceeded. The timing of periods when ψ in the soil exceeds ψ_b determines the timing of seedling emergence. In most species radical extension growth is less sensitive to moisture stress than radicle emergence from the seed, and the radicle also enters moister soil as it grows downwards. As explained previously, germination also depends on temperature and requires a certain quantity of thermal time, Θ.

Under field conditions both temperature and soil water potential vary unpredictably, but under good horticultural practice seeds are sown into moist soil and initial imbibation is rapid. Once imbibed, a seed can progress towards germination provided it remains above ψ_b. Therefore, if ψ is above ψ_b progress towards germination occurs according to a simple thermal time model (Eqn 4.6). If ψ falls below ψ_b, germination cannot occur until either rainfall or irrigation increases ψ above ψ_b again. The thermal time for germination differs for different percentiles of the seed population: for example, the 10th, 50th and 90th percentiles required 55, 77 and 111°C day, respectively (above base 1.4°C) in the experiments of Finch-Savage and Phelps (1993). Hence, the germination and consequently the emergence of seedlings is spread over time and, if soil water potential falls below 1.1 MPa within this range of thermal time, only the lower percentiles will emerge until soil water potential increases again above 1.1 MPa. This results in the flushes of emerging seedlings that are frequently observed in seedbeds that dry out and are then re-wetted and a step-like graph of the percentage emergence *versus* time (see Fig. 4.13).

Timing a light irrigation (e.g. 12–15 mm of water) to occur when sufficient thermal time has elapsed for the initially imbibed seeds to be ready to germinate results in consistently higher percentage emergence and reduced spread of emergence time than pre-sowing irrigation or no irrigation of the seedbed. Irrigation at about 90°C day above a base of 1.4°C means that most seeds will be advanced to the point where they can germinate when ψ exceeds ψ_b (see Fig. 4.14a, b). Unnecessary irrigations are best avoided as they can damage soil structure and thereby make conditions less favourable for emergence, so it is useful to optimize the timing of irrigation using this model. The same principles, with a very similar day-degree requirement for timing irrigation, have been shown to apply to leek (Finch-Savage and Steckel, 1994).

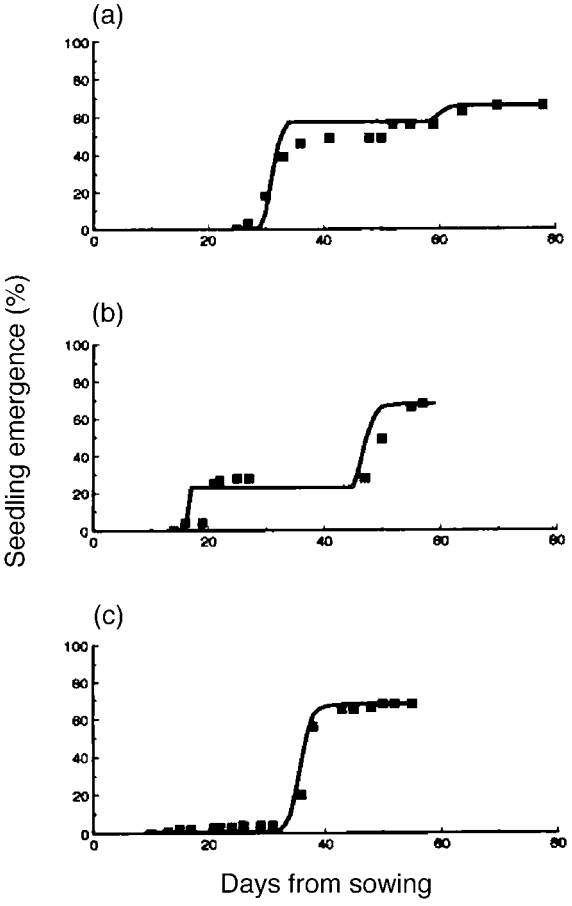

Fig. 4.13. The observed onion seedling emergence from a sandy loam soil at Wellesbourne, UK from sowings made on 23 March (a), 5 April (b) and 17 April (c) 1984 and the emergence predicted by a model based on thermal time and a critical minimum soil water potential for root emergence from seeds (lines). Water potentials and temperature round the seeds were calculated using another model developed for this site that uses daily mean temperature and rainfall as input data. The fitted lines were constrained to the maximum emergence observed in the field (from Finch-Savage and Phelps, 1993. Courtesy of *Journal of Experimental Botany*).

The growth of seedlings after germination but before emergence from soil

As with germination, the rate of elongation of the cotyledon and primary root depends on temperature and water potential but, in soil, mechanical impedance also affects elongation. Figure 4.15a shows the linear relation between temperature above a base temperature of 1.4°C and the rate of cotyledon elongation of onion before formation of the cotyledon hook (Wheeler

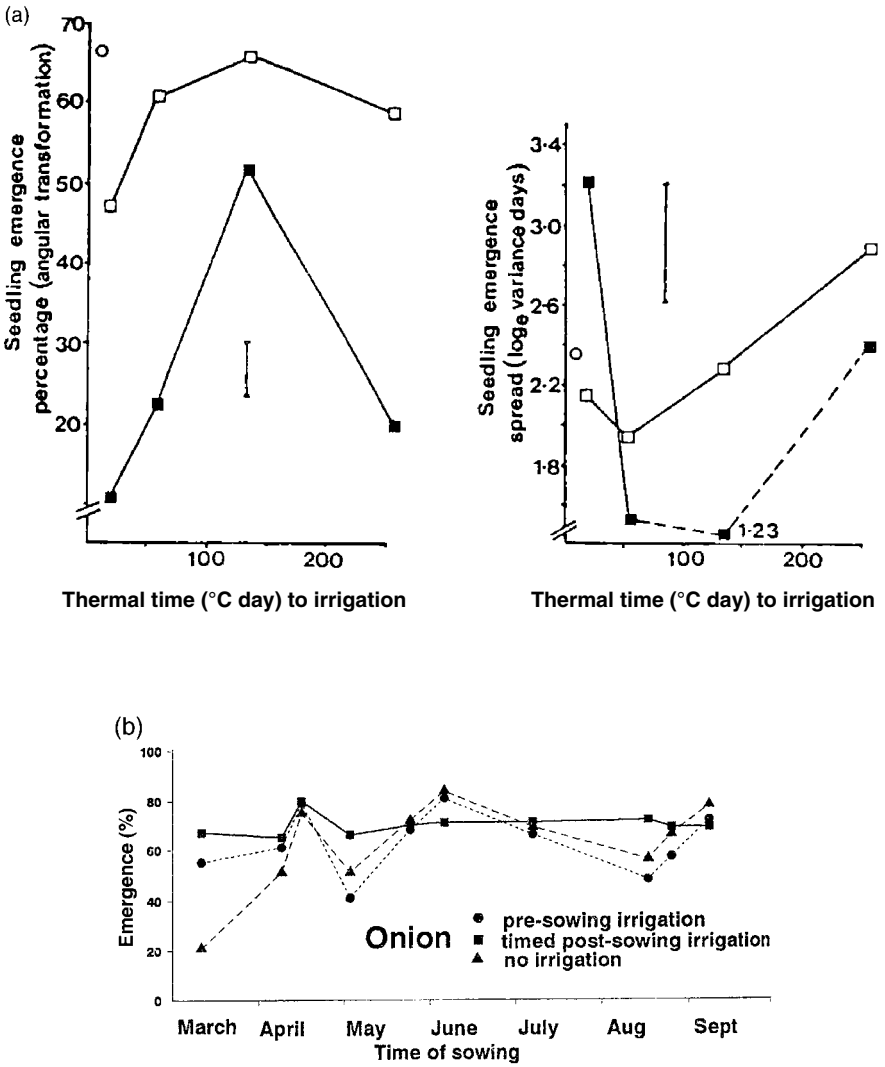

Fig. 4.14. The effects on onion seedling emergence of optimizing the timing of irrigation to coincide with the thermal time required for root emergence from the majority of seeds. (a) The effect of 15 mm of irrigation applied at different thermal times (base 0°C) on the percentage and time spread of seedling emergence in onions sown into moist (□) and dry (■) soil and into moist soil without further irrigation (○). The vertical bars are standard errors with 60 d.f. (from Finch-Savage, 1990. Courtesy of *Acta Horticulturae*). (b) The percentage onion seedling emergence from ten sowings given 15 mm irrigation before sowing, at a thermal time of 90°C day (base 1.4°C) or given no irrigation (from Finch-Savage and Steckel, 1994. Courtesy of *Acta Horticulturae*).

and Ellis, 1991). After hook formation, cotyledon extension growth is exponential and the relative rate of extension growth is linearly related to temperature above the same base temperature (see Fig. 4.15b). The primary root also elongates exponentially, and the relative root extension rate is linearly related to temperature above a base of 3.1°C (see Fig. 4.15c; Wheeler and Ellis, 1994).

These relationships applied over the temperature range 5–20°C, and therefore to emergence in spring-sown crops in temperate regions. They were derived from seedlings with cotyledons up to 25 mm long and roots up to 30 mm

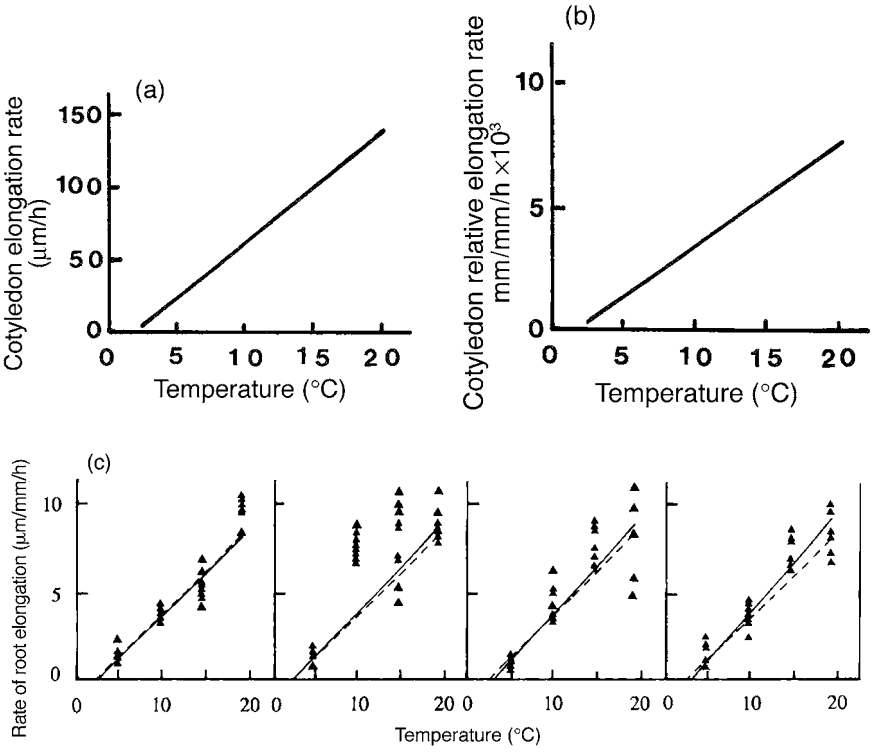

Fig. 4.15. The effects of temperature on seedling elongation rates after germination. (a) The relationship between temperature and cotyledon elongation before hook formation for newly germinated onion seedlings cv. 'White Lisbon' (from Wheeler and Ellis, 1991). (b) The relationship between temperature and the relative rate of elongation after hook formation for the same seedlings as in (a). (c) Relationships between the relative rate of root elongation and temperature for the 20th, 40th, 60th and 80th germination percentiles from a seedlot of onion cv. 'White Lisbon'. The solid lines are linear regression of best fit for all percentiles from three different seedlots; the broken lines are the individual linear regressions for each data set (from Wheeler and Ellis, 1994. Courtesy of *Seed Science and Technology*).

long growing on wet tissue (i.e. without water stress or impedance) in the dark. The similarity of base temperatures, and the linearity of relations between germination rate and elongation rate and temperature in the range 0–20°C, means that thermal time is appropriate for quantifying either stage or the combination of both to give emergence, as the thermal time to emergence studies discussed previously illustrate – e.g. Wagenwoort and Bierhuizen (1977).

As elongation proceeds further and seed reserves run out, cotyledon and root relative growth rates decrease, and lengths reach a maximum of about 50 mm for shoots and 60 mm for roots (Whalley *et al.*, 1999). Differences in seed quality, as manifested by differences in rates of germination and percentage germination between seed-lots, do not affect these relationships, indicating that differences in rate of emergence of normal seedlings from soil between seed-lots are the result of differences in the rate of germination but not of post-germination elongation rate. In addition, relative growth rate of seedlings after emergence is not affected by differences in seed quality (Ellis, 1989). Lower weights of seedlings from poor-quality seed are therefore wholly due to slower germination giving later emergence, and not to any differences in pre- or post-emergence growth rates.

In soil, the water potential around seeds will be reduced both by the reduced matric potential, which becomes increasingly negative as soil dries, and the osmotic potential of the soil solution, which can be damaging if excessive fertilizer – particularly nitrate – is applied (Hegarty, 1976; Greenwood *et al.*, 1992). Figure 4.16 shows that the rate of onion emergence decreases linearly as soil water potential decreases in the range 0 to –0.8 MPa and that percentage emergence declines slightly in this range, but rapidly drops to zero over the range –0.8 to –1.1 MPa.

Onion cotyledon and root elongation have been studied using seeds sown 40 mm deep in moist sand loaded by weights applied to the sand surface so as to give different degrees of mechanical impedance to root penetration (Whalley *et al.*, 1999). Mechanical impedance was quantified by the pressure needed to drive a 2 mm-diameter pointed probe at 1 mm/s through the sand. Compared with unimpeded elongation on moist tissue paper, mechanical impedance greatly decreased both the rate and final extent of cotyledon and root elongation (see Fig. 4.17a, b). The effect was greater for shoots than roots. Cooler temperatures slowed the shoot growth rate (see Fig. 4.18). Subjecting the elongating seedlings to an osmotically generated water stress in addition to mechanical impedance reduced potential elongation further (see Fig. 4.19). Shoots of seedlings subjected to mechanical impedance for a period and then transferred to grow on moist tissue in the absence of impedance elongated rapidly after removal of the impedance. Roots had a much smaller capacity for such recovery than shoots. The extent of recovery of shoot length, compared with seedlings grown throughout without impedance, decreased as the impedance applied increased or the duration of impedance increased, but shoots were still able to make some elongation after 35 days of impedance at 20°C (see Fig. 4.20). Roots responded similarly, but with a proportionally less extensive recovery ending after a shorter period compared with shoots.

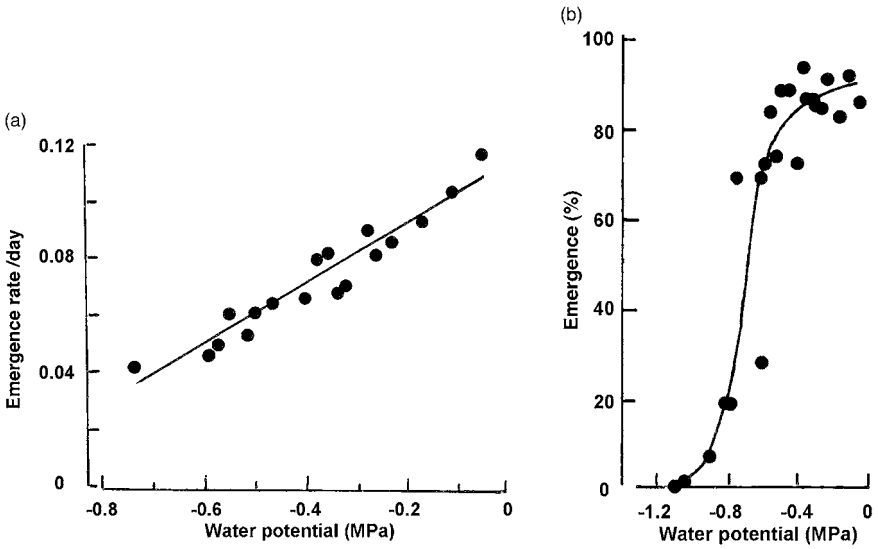

Fig. 4.16. The effect of soil water potential on the rate (a) and the percentage (b) of emergence of onion seeds at 15°C. The rate was measured as the reciprocal of the time to reach 50% of the final number emerging. The differences in soil water potential were caused by differences in osmotic potential rather than matric potential (redrawn from Hegarty, 1976).

The results of these experiments were summarized by a quantitative model expressed by Equations 4.14 and 4.15:

Rate of elongation in thermal time =

$$dL/d(t-t_g) = b(1-\psi/\psi_L)(1-(q/q_L)^n)[A(t-t_g)(1-\psi/\psi_L)(1-(q/q_L)^n)-L]$$ (Eqn 4.14, see Table 4.4 for explanation of symbols).

The maximum shoot length attainable decreases if the shoot is slowed or prevented from growth by mechanical impedance (see Fig. 4.20). This is likely to be due to the depletion of seed reserves and the rate of depletion to depend on temperature, and therefore a function of thermal time is appropriate to model the effect. To account for this, the term $A(t - t_g)$ in Eqn 4.13 decreases as thermal time elapses, according to Eqn 4.15:

$$A(t-t_g) = C / (1 + [(t-t_g)/d)]^m)$$ (Eqn 4.15)

where

d = fitted constant, value 356°C day (base 2.1°C)

C = fitted constant, value 83.16 mm

m = dimensionless scaling parameter, value 1.735

A, t and t_g are as defined for Eqn 4.14.

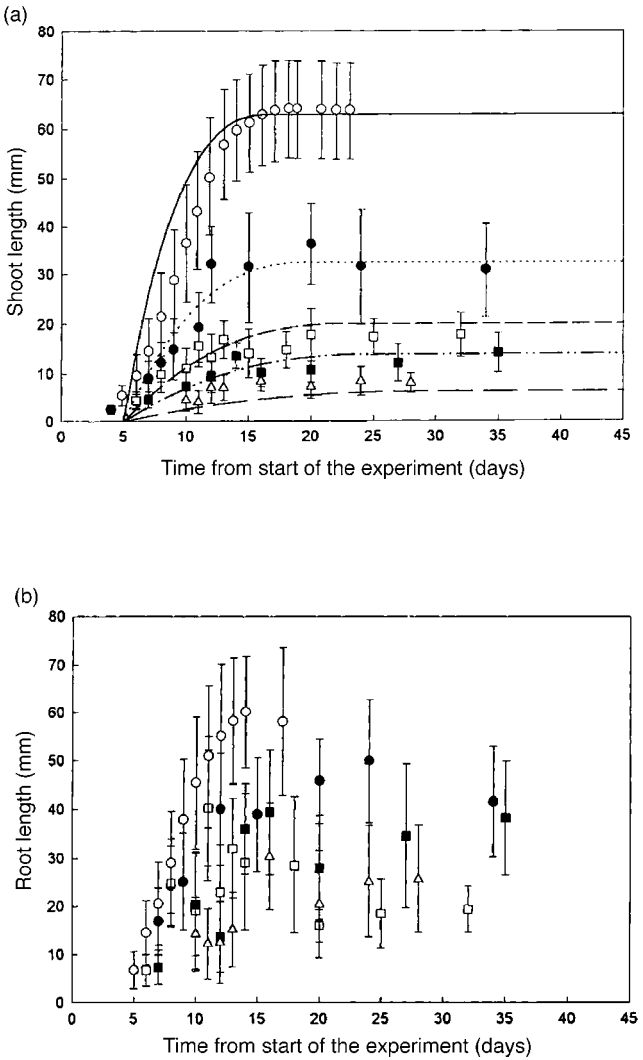

Fig. 4.17. The effects of mechanical impedance on the elongation of emerging onion seedlings. (a) The shoot length of onion seedlings growing at 20°C in environments of constant strength: on sloping filter paper (○); in sand cultures with pressure resistances to a penetrometer of 0.19 (●), 0.39 (□), 0.53 (■) and 0.75 (△) MPa. The bars indicate the standard deviations for the means, which were based on 30 replicates of each treatment. The curves shown were obtained using Eqn 4.12. (b) The growth in root length for the same as seedlings in (a) (from Whalley *et al.*, 1999. Courtesy of *Plant, Cell and Environment*).

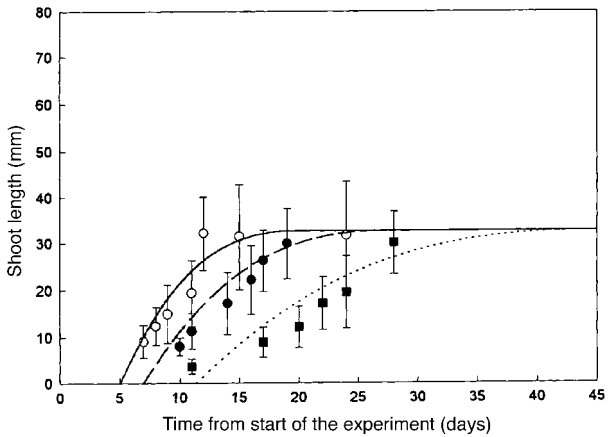

Fig. 4.18. Combined effects of temperature and mechanical impedance on the elongation of emerging onion seedlings: the shoot length of seedlings growing in sand with a penetrometer pressure of 0.19 MPa at 10 (■), 15 (●) or 20°C (○). The curves shown were obtained using Eqn 4.12 (from Whalley *et al.*, 1999. Courtesy of *Plant, Cell and Environment*).

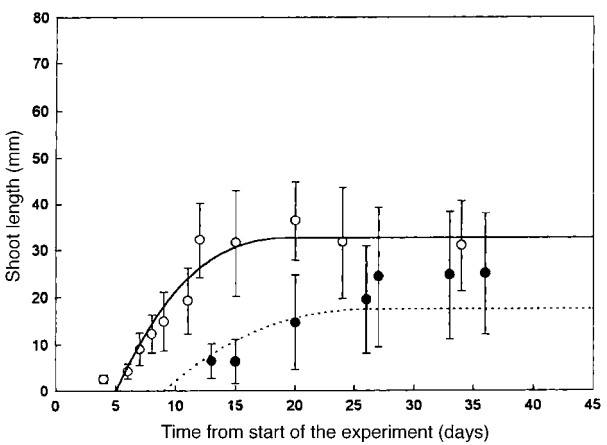

Fig. 4.19. Combined effects of mechanical impedance and water (osmotic) stress on the elongation of emerging onion seedlings: the shoot length of seedlings growing in sand with a penetrometer pressure of 0.19 MPa with either –30 kPa water potential (○) (just to avoid saturation and ensure aeration) or a water stress of –0.4 MPa (●) induced by polythene glycol of high molecular weight. The curves shown were derived using Eqn 4.12, with a delay in germination for the water-stressed seed calculated using a germination model (from Whalley *et al.*, 1999. Courtesy of *Plant, Cell and Environment*).

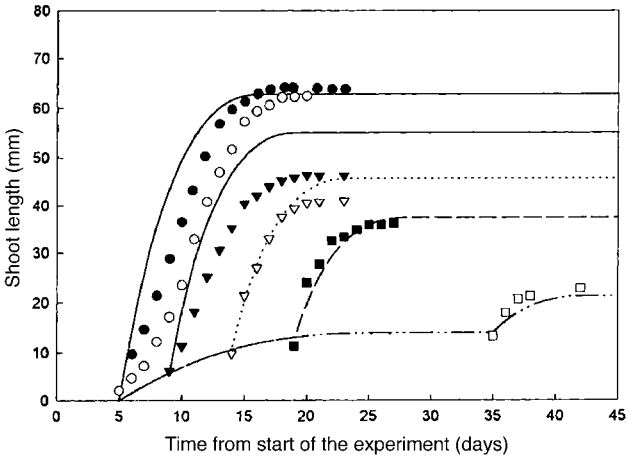

Fig. 4.20. The recovery of elongation growth in onion shoots on sloping filter paper following exposure to mechanical impedance in sand equivalent to 0.53 MPa penetrometer pressure for 0 (●), 5 (○), 9 (▼), 14 (▽), 19 (■) or 35 days (□). The curves shown were obtained using Eqn 4.12. Only one curve is shown for the 0 and 5 day treatments since time to germinate is 5 days at 20°C (from Whalley *et al.*, 1999. Courtesy of *Plant, Cell and Environment*).

Table 4.4. Explanation of symbols in Eqn 4.14.

Symbol	Value	Units	Definition
t		°C day	Thermal time since start of germination (base temperature 2.1°C)
t_g	90	°C day	Thermal time needed to germinate
b	0.01044	°C day	A fitted constant
L		mm	Shoot length
A	67	mm	Maximum shoot length in the absence of mechanical impedance
ψ		MPa	Water potential in soil
ψ_L	1.1	MPa	Water potential that just prevents elongation
q		MPa	Mechanical impedance measured by penetrometer (see text above)
q_L	1.111	MPa	Mechanical impedance that would just prevent extension growth
n			Dimensionless scaling parameter

The lines in Figs 4.17 and 4.20 were fitted using the data points shown to find values for the constants in the equations, but the line in Fig. 4.19 is a predicted response using this model.

These equations indicate factors important in determining the rate of seedling elongation in soil prior to emergence and show how temperature, time, water potential and mechanical impedance affect this. How the elongation rate responds to changes in these physical properties as the soil changes in temperature and moisture content can be predicted. It should be noted that impedance is not an absolute measure, i.e. independent of the instrumentation used to measure it, unlike temperature or water potential.

The importance of mechanical impedance to field emergence is illustrated by a study on onions sown 20 mm deep in a sandy loam soil at a sequence of dates and then subjected to the press-wheel compaction pressures of 0, 2.8 or 8 N/cm^2 either with or without a subsequent 5 mm irrigation. Percentage emergence decreased linearly as soil impedance increased (see Fig. 4.21), and this relationship explained over 80% of the variation in percentage emergence. Here, impedance was measured as the work done in driving a 2 mm-diameter flat-ended probe 15 mm into the soil in 20 s. Excavations showed that pre-emergence losses were almost wholly due to failure of seedlings to emerge through the soil after germination, rather than failure to germinate.

Seeds sown below the soil surface must inevitably overcome some mechanical impedance to emerge, but the degree of impedance can vary greatly with soil and weather conditions. Impedance can increase because of soil compaction, the slumping of poorly structured soil or because of the formation of a surface crust caused by rain and subsequent drying.

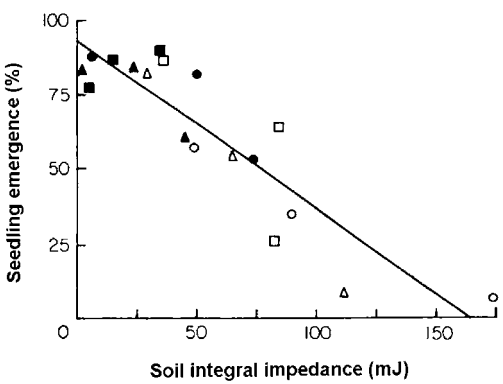

Fig. 4.21. The relationship between percentage onion seedling emergence and the integral impedance of the soil to penetration (equivalent to the work done (mJ)) by a 2 mm-diameter flat-ended penetrometer driven to depth of 15 mm at a constant rate for 20 s (from Hegarty and Royle, 1978. Courtesy of *Journal of Applied Ecology*).

Newly germinated seedlings subjected to water potentials sufficient to prevent root or shoot elongation were able to fully maintain their elongation potential for 35 days at 20°C (Whalley *et al.*, 2001). This contrasts with seedlings prevented from elongating by mechanical impedance, which lose most of their capacity to elongate over 35 days (see Fig. 4.20).

VEGETATIVE GROWTH

Seedling growth rates

As with germination and emergence, the growth rate of seedling alliums after emergence is slow compared with most crop species. However, many non-crop species are slower growing, particularly woody species and those adapted to non-productive environments (Brewster, 1979). Table 4.5 compares the Relative Growth Rate (RGR) of species growing in near-optimal temperatures during the exponential, seedling phase of growth with that of onion. From Table 4.5 it is clear that onion is the fastest growing of the edible alliums studied, but that the RGR of onion is only about half that of spring cabbage or lettuce. This means that, starting at the same weight and growing under the same conditions, onion will take nearly twice as long as spring cabbage or lettuce to reach a given weight.

Growth rates are strongly dependent on temperature. Figure 4.22 shows the relationships between RGR, Relative Leaf Growth Rate (RLGR) and leaf initiation rates and temperature. RGR and RLGR increase linearly over the range 6–20°C, whereas leaf initiation rates have a lower base temperature and increased linearly over the range 3.5–23°C.

Hence, growth rates are given by the simple equations:

$$RGR = 0.0111(T-6) \quad \text{(Eqn 4.16a)}$$

$$RLGR = 0.0108(T-6) \quad \text{(Eqn 4.16b)}$$

Here, RGR and RLGR are in per day, T is temperature in °C and 6°C represents the 'base temperature' (T_b) below which growth ceases. If mean temperatures do not exceed the optimal range, i.e. not above about 27°C (see Fig. 4.22), this relationship implies that growth can be predicted using 'thermal time' as described for predictions of seed germination and emergence (Eqns 4.6 and 4.7). Thus, seedling dry weight and leaf area will be linearly related to accumulated day-degrees between 6 and 20°C. This accords with field studies in which log seedling dry weight was a linear function of accumulated day degrees between 6 and 20°C, whereas leaves initiated increased linearly with day-degrees above 2°C (Brewster *et al.*, 1977). A straight onion cotyledon, at the end of the emergence phase, would typically have a leaf area of about 0.5 cm^2. Using this,

Table 4.5. The relative growth rate (RGR) of seedlings of various species growing exponentially in near-optimal temperatures with abundant water and mineral nutrients, compared with that of onion, cv. 'Hyton' or cv. 'Hygro'. The data come from a number of experiments which varied in the light environment used. To account for this, the absolute values of RGR recorded were 'scaled' relative to a value of unity attributed to onion in each experiment (from Grime and Hunt, 1975; Brewster, 1979; Brewster and Sutherland, 1993).

Species	RGR relative to onion
Stinging nettle[a] (*Urtica dioica*)	2.50
Spring cabbage (*Brassica oleracea* var. capitata cv. 'Hornet')	1.96
Lettuce (*Lactuca sativa* cv. 'Penlake')	1.91
Brussels sprout (*Brassica oleracea* var. gemmifera)	1.69
Cauliflower (*Brassica oleracea* var. botrytis cv. 'White Rock')	1.56
Perennial ryegrass[a] (*Lolium perenne*)	1.49
Carrot (*Daucus carota* cv. 'Nanco')	1.41
Celery (*Apium graveolens* cv. 'Lathom Self-blanching')	1.37
Red beet (*Beta vulgaris* cv. 'Monopoly')	1.34
Onion (*Allium cepa* cv. 'Hyton' or cv. 'Hygro')	1.00
Leek (*Allium ampeloprasum* cv. 'Winterreuzen')	0.89
Leek (*Allium ampeloprasum* cv. 'Early Market')	0.83
Leek (*Allium ampeloprasum* cv. 'Winter Crop')	0.80
Japanese bunching onion (*Allium fistulosum* cv. 'Common Bunching Multi-stalk')	0.85
Chive (*Allium schoenoprasum*)	0.73
Sitka spruce[a] (*Picea sitchensis*)	0.25

[a]Values for these species were estimated indirectly; see Brewster (1979, p.356).

the leaf area of an onion plant that has been growing for a while following emergence can be predicted by the equation:

$$\log_e(\text{leaf area}) = \log_e(0.5) + 0.0108 \times \Sigma DD \qquad \text{(Eqn 4.17a)}$$

and seedling dry weight is predicted by:

$$\log_e(\text{Dry Weight}) = \log_e(W_0) + 0.0111 \times \Sigma DD \qquad \text{(Eqn 4.17b)}$$

ΣDD is the summation of day-degrees between 6 and 20°C accumulated since emergence and W_0 is the dry weight at seedling emergence. Eqn 4.17b with $\log_e(W_o)$ equal to −6.086, indicating a dry weight at emergence of 2.27 mg, applied to field growth of onion seedlings in central UK (Brewster *et al.*, 1977).

A model for growth in seedling shoot dry weight (W) in g, which includes the effects on growth rates of a daily income of photosynthetically active radiation, PAR (R), as well as daily mean temperature (t) – again in terms of accumulated day-degrees above a base temperature (t_b) – was developed by

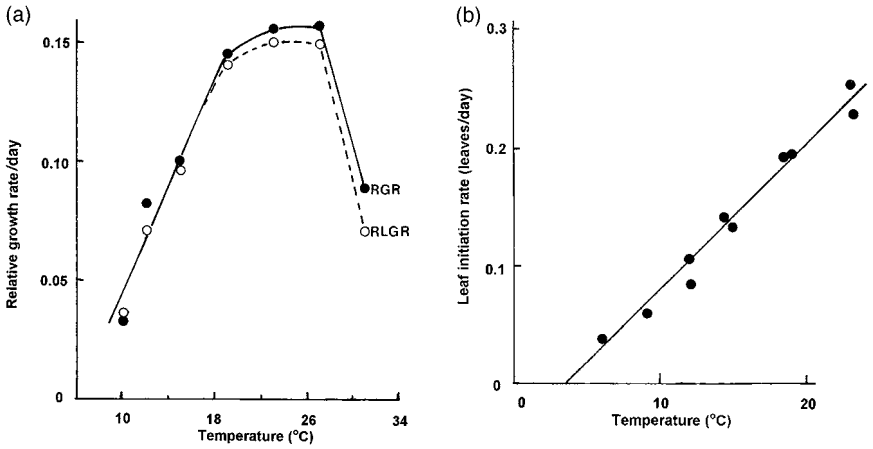

Fig. 4.22. (a) The effect of temperature on the Relative Growth Rate (RGR) of whole plant dry weight (solid symbols) and on the Relative Leaf Growth Rate (RLGR) (open symbols) of cv. 'Hygro' during early exponential growth (from Brewster, 1979). RGR is the rate of increase in dry weight per unit of existing dry weight (RGR = 1/W.dW/dt, where W = dry weight and t = time). Similarly, RLGR is the rate of increase of leaf area per unit of existing leaf area. (b) The effect of temperature on the rate of initiation of leaves by the main shoot apex (i.e. not counting leaves on side shoots) of cvs 'Hygro', 'Hyton' and 'Rijnsburger', all 'Rijnsburger' types, growing in controlled environments (unpublished data).

Scaife *et al.* (1987). Here, 'Effective Day Degrees' (EDD) are used instead of day-degrees (DD) in Eqn 4.17b:

$$\log_e(\text{Dry Weight}) = \log_e(W_0) + p \times \Sigma\ \text{EDD} \qquad \text{(Eqn 4.18)}$$

where p is a parameter that expresses relative growth per EDD and has units per EDD.

An 'Effective Day Degree' is a day-degree adjusted or weighted for the daily total PAR impinging on the plants (termed the 'radiant exposure to PAR'). EDDs are calculated according the equation:

$$\text{EDD}^{-1} = \text{DD}^{-1} + f \times R^{-1} \qquad \text{(Eqn 4.19a)}$$

this can be also expressed in the equivalent form:

$$\text{EDD} = \text{DD}/(1 + (f \times \text{DD})/R) \qquad \text{(Eqn 4.19b)}$$

R is the daily radiant exposure to photosyntetically active radiation, usually expressed as MJ/m^2

f is a parameter that determines sensitivity to PAR levels and has units $MJ/m^2/DD$.

Parameters p and f are characteristic of a species. From experiments under controlled PARs and temperatures, the value for onion of p was 0.0160/EDD, f

was 0.136 MJ/m^2/DD and T_b, the base temperature for growth and calculating DDs, was 5.9°C (Brewster and Sutherland, 1993). An appropriate value for $\log_e W_0$, the log of the shoot dry weight (g) at emergence, is −6.086. The value of f was larger than for other species, indicating greater sensitivity to light income, probably because the leaves are erect and do not intercept a high proportion of PAR in the early stages of growth. The difficulty of growing onions satisfactorily in conditions of low light is a familiar problem to experimenters, who have to raise them in glasshouses during the winter. The value of p was one-half to two-thirds that for faster-growing vegetable seedlings like cabbage and lettuce, indicating an inherently low relative growth rate for onion.

Carbon dioxide concentration and growth and photosynthetic rates

Elevated CO_2 concentrations increase growth in dry weight and leaf area in onions (Daymond *et al.*, 1997; Wurr *et al.*, 1998; Wheeler *et al.*, 2004; Fig. 4.23a, b). At the stage of bulb initiation, the light-saturated rate of photosynthesis in the youngest fully expanded leaf was greater in onions grown at 560 rather than at 350 μmol/mol CO_2, particularly in plants grown in warmer temperatures (see Fig. 4.24). A higher photosynthetic rate was probably the basis of the faster growth at elevated CO_2. During darkness, CO_2 concentrations of 0.6% have been measured in the air within the hollow cavity of onion leaves, about eight times the level in ambient air, presumably as a result of the retention of respiratory CO_2 (Darbyshire *et al.*, 1979). This might conserve respired CO_2 and 'recycle' it in photosynthesis with the onset of light.

Water relations of growth and photosynthesis

Leaf relative growth rates and stomatal conductance decline as leaf water potential and the associated turgor pressure decline (see Fig. 4.25). The maximum turgor pressure developed within onion leaves was found to be 0.4 MPa, rather low compared with other crop species, where a maximum turgor of 1 MPa is common. Stomatal conductance decreases rapidly when turgor declines from 0.15 to 0.05 MPa, the rate of decline being three times faster than in *Phaseolus* beans over the same range of turgor (Millar *et al.*, 1971). Therefore, both transpiration and photosynthesis will drop rapidly with such decreases in turgor. When the roots of onion plants are exposed to saline solutions, the plants compensate for the increased osmotic potential in the root medium by increasing the leaf osmotic potential by only about half as much. Hence, leaf turgor is reduced in such a saline solution. In contrast, bean and

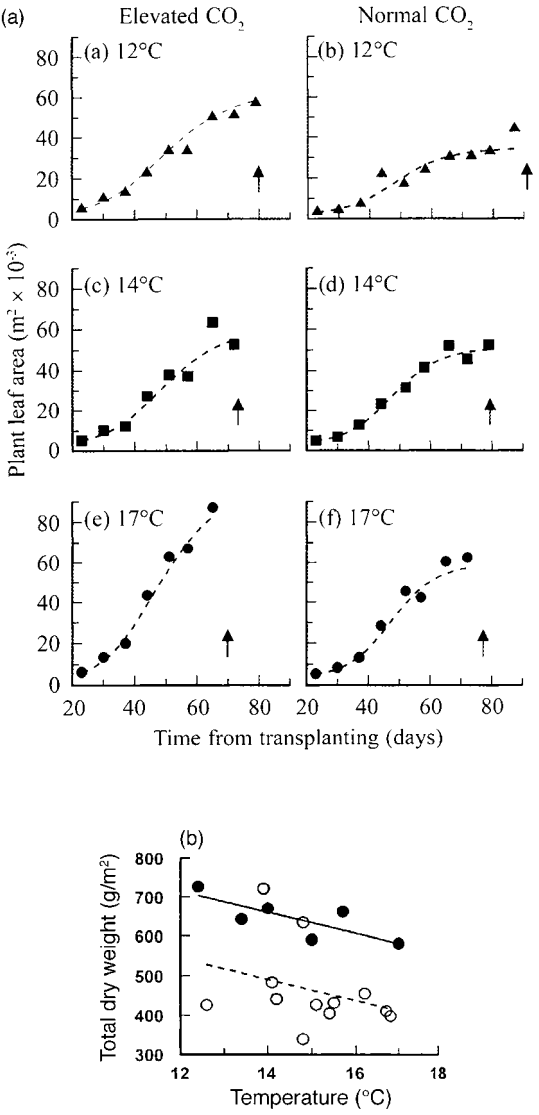

Fig. 4.23. (a) The relationship between total plant leaf area and time from transplanting in onion cv. 'Hysam' at different temperatures under elevated and normal CO_2 concentrations (532 and 374 μmol/mol CO_2, respectively). The arrows denote the time of bulbing. The points are the means of nine replicates and the lines are fitted logistic curves (from Wheeler *et al.*, 2004. Courtesy of *Annals of Applied Biology*). (b) The relationship between total crop dry weight of onion cv. 'Hysam' at the time of bulbing and the mean temperature from transplanting to bulbing at elevated (●) and normal (○) CO_2 concentrations (from Daymond *et al.*, 1997. Courtesy of *Journal of Horticultural Science*).

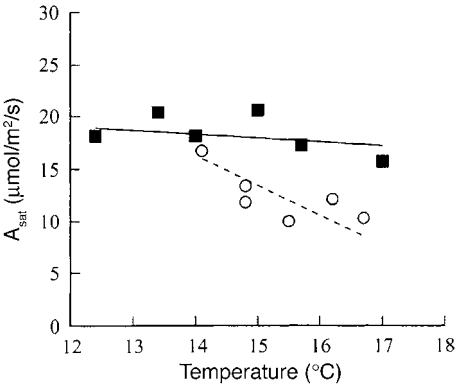

Fig 4.24. The relationship between the light-saturated rate of photosynthesis (A_{sat}) at the time of bulbing and mean growth temperature from transplanting to bulbing for plants grown at elevated (■) or normal (○) CO_2 concentrations (532 and 374 μmol/mol CO_2, respectively) and measured at 560 (■) or 350 (○) μmol/mol CO_2 (from Wheeler *et al.*, 2004. Courtesy of *Annals of Applied Biology*).

cotton plants in the same situation increase their leaf osmotic potential to compensate fully for increases in the root medium, and their turgor is not reduced (Gale *et al.*, 1967). The decrease in leaf turgor induced in onion reduces the photosynthetic rate of the leaves, the effect being larger the higher the evapotranspirative demand on the leaves. These changes in turgor and photosynthetic rate are quickly reversed by transferring the plants back to non-saline solution.

In summary, onion plants have less ability to compensate for decreases in the water potential of the root medium by parallel decreases in the leaf water potential than do other crop species. This causes leaf turgor pressure to decline rapidly as the water potential of the root medium declines and this, in turn, decreases leaf expansion rate, photosynthetic rate and, ultimately, crop growth rate. Studies in saline solutions indicated a 50% lowering of growth by a sodium chloride solution of osmotic pressure 0.125 MPa, whereas for cabbage, lettuce and beans an equivalent growth reduction required an osmotic pressure of 0.4 MPa (Bernstein and Hayward, 1958). In addition, the root system of onions is rather shallow, sparse and lacking root hairs (see Chapter 2, 'The Root System'). Consequently, water extraction is confined mainly to the top 25 cm of soil (Goltz *et al.*, 1971).

These physiological and morphological traits indicate that the photosynthetic rate and the growth rate of onion are more sensitive to water stress than the majority of crops. On the other hand, observations on plants growing in arid conditions show that they can survive long periods of water stress, making no growth, but ultimately recovering when water becomes available (Levy *et al.*, 1981). Furthermore, onion roots can remain alive in the absence of

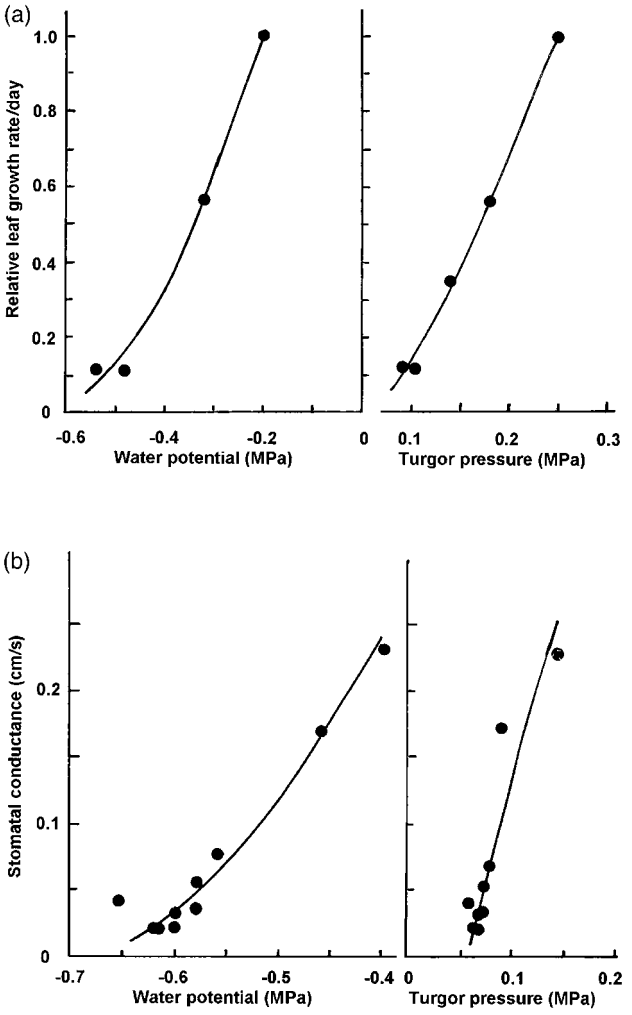

Fig. 4.25. (a) Relative growth rate of onion leaf length at 25°C as a function of leaf water potential and of turgor pressure (redrawn from Fig. 9 of Millar *et al.,* 1971). (b) Stomatal conductance of onion leaves at 25°C as a function of leaf water potential and of turgor pressure (redrawn from Fig. 7 of above source).

any free water around them for up to 200 days (see Fig. 2.13e) (Stasovski and Peterson, 1993). The bulbing habit may have evolved in the ancestors of onions as a strategy to survive summer drought. As with other features, like the low relative growth rate and the low-growing, upright leaves, the water relations of the onion suggest evolution from ancestors with stress-tolerant rather than competitive traits (Grime, 2002).

Stomatal physiology

Stomatal opening in onion, as with other species, involves the electrochemical pumping of potassium K^+ ions into the stomatal guard cells, causing an increase in their osmotic pressure and turgor. Because the guard cells lack starch granules, the influx of K^+ cannot be electrically balanced by the generation of negative malate ions from starch, as occurs in many species. Instead, chloride, Cl^- enters the guard cell along with the K^+ and maintains electroneutrality (Schnabl and Raschke, 1980). Hence, chloride is important in plant nutrition (see Chapter 6). Potassium uptake by guard cells correlates with the morning opening of stomatal apertures, but in the afternoon K^+ levels decline and an increase in sucrose concentration in the guard cells maintains turgidity and open apertures (Amodeo *et al.*, 1996).

The sudden leaf necrosis, termed 'onion blast', involves stomata. This results from ozone damage to leaves when atmospheric conditions result in high ozone concentrations. Onion cultivars differ in sensitivity to ozone damage. Resistant varieties are in fact hypersensitive and, under high concentrations of ozone, the membranes of their stomatal cells become leaky. This causes rapid stomatal closure and thereby prevents the entry of ozone inside the leaves and consequent damage to the mesophyll cells (Eagle and Gableman, 1966).

ONION BULBING

The estimation of bulb initiation

A feature that unequivocally indicates that bulbing has started is the development of leaf initials into bladeless 'bulb scales'. This can be diagnosed as the first occurrence of a 'leaf ratio' (leaf blade length:sheath length) of less than unity (Heath and Hollies, 1965; Fig. 4.26). Where many plants are available for sampling, scale initiation can be quite quickly estimated from examining plants sliced longitudinally upwards through the centre of the sheath. Mean dates of bulb initiation can be estimated from a series of such samples (de Visser, 1994a).

Normally, a leaf ratio below unity is coincident with marked swelling of the outer leaf sheaths and a consequent rapid increase in 'bulbing ratio' (maximum bulb diameter:minimum sheath diameter). This latter ratio has been more commonly used in bulbing studies, since it can easily be measured non-destructively, whereas the assessment of minimum leaf ratio involves the dissection of plants and is more laborious.

However, the occurrence of the first leaf ratio less than unity is not invariably linked with the attainment of a particular bulbing ratio. Bulbing ratios greater than 2, commonly used to define bulb initiation, can occur in the absence of bulb

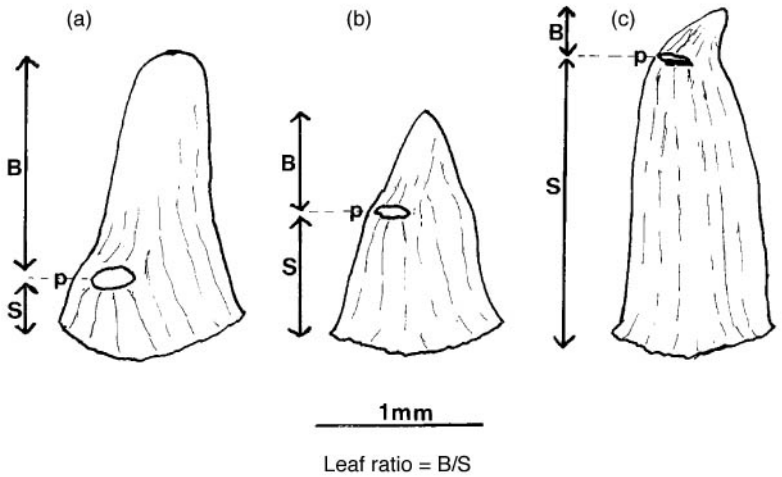

Fig. 4.26. The appearance of developing leaf initials during leaf blade growth (a), early-stage bulbing (b) and established bulbing (c). p is the pore through which the blade of the next leaf emerges from its encasing sheath during leaf growth. Bulbing is characterized by a decrease in the ratio of blade length, B to sheath length, S, termed the 'leaf ratio'. Initials with B/S below unity are termed 'bulb scales' (Heath and Hollies, 1965).

scale development in N-deficient plants (Brewster and Butler, 1989). In field-grown plants grown at densities of 25 and 400/m^2, bulbing started 8 days sooner at 400/m^2 when measured by bulbing ratio, whereas bulb scales were initiated 23 days earlier in the plants at this high density than at 25/m^2 (Mondal *et al.*, 1986a).

Conditions favouring carbohydrate accumulation within the plant can lead to thickened leaf sheaths and increased bulbing ratios without formation of bulb scales. In addition, leaf initials differentiate into bulb scales on lateral shoots before this occurs on the main shoot axis. As a result, in cultivars and in conditions that produce many side shoots, a high bulbing ratio can occur long before the main axis stops producing green leaves (Wiles, 1989).

Because of this variability in the linkage between increases in bulbing ratio and decreases in leaf ratio on the main shoot, and because a decrease in leaf ratio is the first indication of the initiation of the storage scales that ultimately results in the cessation of leaf blade growth and the ripening of bulbs, a decrease in minimum leaf ratio below unity on the main shoot axis is the preferable method of defining bulb initiation. Since leaf initiation rates are temperature dependent (see Fig. 4.22b), it is possible to use thermal time to estimate leaf initiation date from leaf number, and hence estimate the date of initiation of the first bulb scale from a sample taken after the event (Brewster, 1997b).

The bulbing ratio can be measured non-destructively and can therefore be determined repeatedly on the same plant. If treatment comparisons are made which avoid the complications discussed above – for example, for comparing cultivars growing under the same conditions at a similar plant density – it is a useful technique for assessing bulbing. The precision of determining the start of bulbing from such measurements has been improved by graphing the cumulative sum of (bulbing ratio minus 1.2) against sample date – a technique termed 'cusums', derived from quality control statistical methods. Upturns from a line following the *x*-axis clearly indicate the start of bulbing (Lancaster *et al.*, 1996).

The partitioning of dry matter during bulbing

Prior to bulbing, while the leaf canopy is developing, about 74% of the shoot dry matter growth is partitioned into leaf blades and the rest into stem bases and leaf sheaths (de Visser, 1994a; Tei *et al.*, 1996). After bulb scales have initiated, previously differentiated leaf blades are still expanding, so there is a transition period while the partitioning of shoot dry matter growth to leaf blades decreases from 74 to 0%, and all new growth goes to the storage scales. This partitioning is well described by a Gompertz equation (see Fig. 4.27). The rapidity of the transition in partitioning will vary with the development rate, which is determined by temperature (de Visser, 1994a; Daymond *et al.*, 1997).

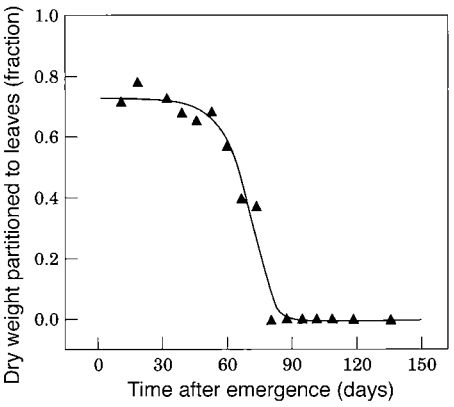

Fig. 4.27. The fraction of dry matter production partitioned to leaf blades in an April-sown onion crop growing at Wellesbourne, UK, showing the decline to zero following bulb initiation. The fitted line is a Gompertz curve (from Tei *et al.*, 1996. Courtesy of *Annals of Botany*).

The control of bulbing by photoperiod and temperature

As indicated by Tables 4.1 to 4.3, the timing of bulb initiation in relation to leaf canopy development is critical in determining yields in bulb-forming alliums. An understanding of what controls bulb initiation is therefore important. Garner and Allard (1920) first showed that onions develop bulbs in response to long photoperiods, and later it was shown that onion varieties grown at different latitudes could be distinguished by the minimum day-length needed to induce them to bulb (see Chapter 1 'Onion Cultivars'). Further research showed that, in a given day-length, bulbing was faster the higher the temperature. These effects of photoperiod and temperature have since been confirmed by many studies (Brewster, 1990a). Onion leaves must be exposed continuously to bulb-inductive photoperiods in order to complete bulbing. If bulbing plants are transferred to short, non-inductive photoperiods green leaf production can resume, even in plants at an advanced stage of bulb development (see Fig. 4.28).

Photoperiod and temperature responses have been quantified for two cultivars grown in the UK, 'Hyton' used for spring sowings and 'Keepwell' for autumn sowings (see Figs 4.29a and 4.30). These data were obtained by regularly sampling plants growing in constant photoperiods and temperatures and determining when bulb scales first appeared. The interval between transfer of plants to test photoperiods and when bulb scales were initiated measured the time needed for bulbing, and the reciprocal of this time was taken as the measure of 'rate of bulbing'.

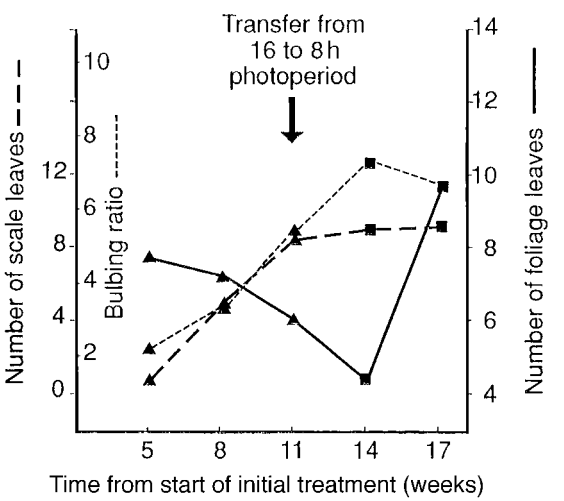

Fig. 4.28. The reversal of bulbing in onion cv. 'Rocket' at an advanced stage of bulbing, following transfer from 16 to 8 h photoperiods. Note the resumption of foliage leaf production even though many bulb scales had formed (redrawn from Wright and Sobeih, 1986).

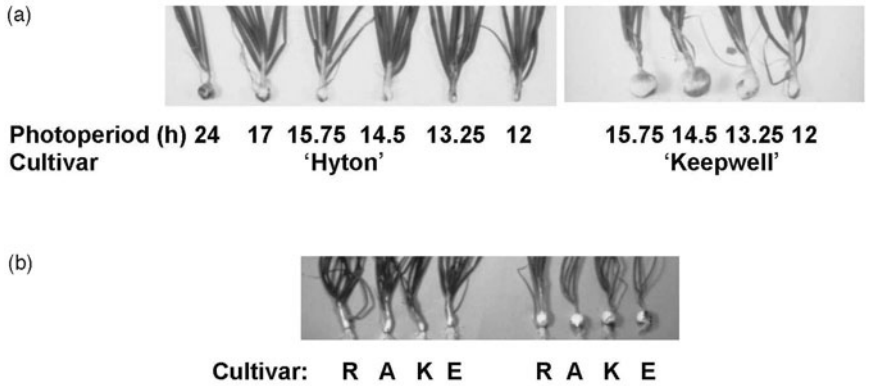

Fig. 4.29. Responses of onion bulbing to light conditions. (a) Bulbing of cv. 'Hyton', a Dutch long-day hybrid for spring sowing, and cv. 'Keepwell', a Japanese intermediate-day hybrid, autumn-sown in the UK, after 70 days at a range of constant daylight photoperiods. (b) Four cvs of decreasing day-length requirement for bulbing, R > A > K > E, after 40 days in 18 h photoperiods of light of red:far-red ratio (RFR) 2.2 (left group) or 0.65 (right group) (Mondal *et al.*, 1986b. Photographs courtesy of Warwick HRI).

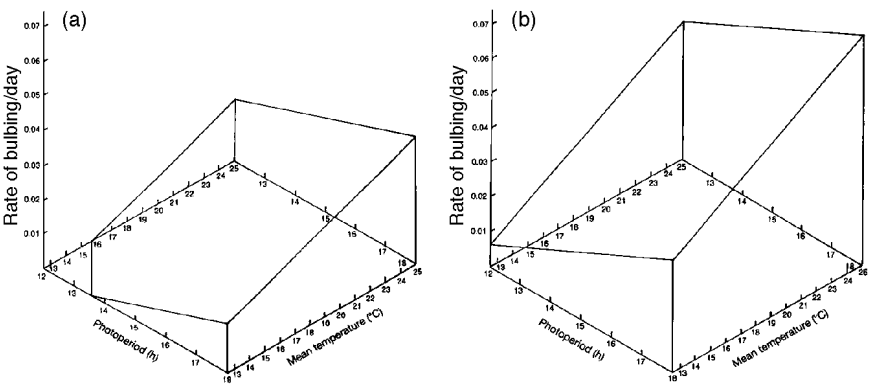

Fig. 4.30. Relationships between the rate of onion bulbing and photoperiod and temperature for the spring-sown cv. 'Hyton' (a) and the autumn-sown cv. 'Keepwell' (b) derived from experiments in a range of daylight photoperiods and controlled temperatures (see plants in Fig. 4.29a). Rate of bulbing was calculated as the reciprocal of the time (days) for the first bladeless bulb scales (see Fig. 4.26) to be detectable.

Using these data it was shown that, for cv. 'Keepwell':

$$\text{Rate of bulbing} = -0.079 + 0.0043 \times \text{Photoperiod} + 0.0027 \times \text{Temperature} \quad \text{(Eqn 4.20)}$$

and for cv. 'Hyton':

$$\text{Rate of bulbing} = -0.066 + 0.0032 \times \text{Photoperiod} + 0.0018 \times \text{Temperature} \quad \text{(Eqn 4.21)}$$

Here, rate of bulbing was day, photoperiod in h and daily mean temperature in °C. These equations show that rate of bulbing, when measured in this way, is proportional to both photoperiod and temperature, with the response being more acute for 'Keepwell' than for 'Hyton'.

Substituting natural photoperiods and daily average temperatures, as recorded at Wellesbourne, central England, into these equations gives the prediction that cv. 'Hyton' will initiate bulb scales on 7 July whereas cv. 'Keepwell' will initiate bulb scales on 7 June if both are planted on 1 May. Leaf blade growth will slow after bulb scale initiation. Substituting recorded temperatures for Wellesbourne into Eqn 4.17a indicates that a crop emerging on 1 May with a plant population of 60 plants/m^2 will achieve a LAI of 3.2 and therefore a light interception of 60% (see Fig. 4.1) by 6 July in an average season. Such a crop will therefore have the potential for a high yield provided that leaf growth can continue until 6 July. Cv. 'Hyton' therefore seems well adapted and will have a higher potential yield than cv. 'Keepwell' if both are sown in spring.

In a trial comparing cv. 'Keepwell' and cv. 'Rijnsburger-bola' (a cv. very similar to 'Hyton' in season of bulbing), both sown on 28 February, the latter yielded 41 t/ha, with 25 t/ha of bulbs greater than 45 mm diameter, and was mature on 20 August, whereas the former yielded only 24 t/ha, with none larger than 45 mm, and was fully mature on 9 July (Salter, 1976). This illustrates in practice the critical importance of the response of bulbing to photoperiod and temperature in determining the yield potential of a cultivar at a given location. The response must be appropriate for the natural photoperiods and temperatures of the locality, in that it must permit sufficient leaf growth to occur before bulbing starts.

Cultivar 'Keepwell' is grown as an overwintered crop and will typically produce a leaf area of about 25 cm^2 per plant in early March from a sowing made in mid- to late August at Wellesbourne. From Equation 4.17a we can calculate that the leaf area per plant will reach 442 cm^2 by 31 May in an average year at Wellesbourne, when Equation 4.20 indicates that bulbs will be initiated. If the plant population is 60 plants/m^2 this implies a leaf area index of 2.65 which, according to Eqn 4.1, would intercept 54% of the incoming light. Thus, when grown from a late-summer sowing, cv. 'Keepwell' is well adapted to produce a satisfactory bulb yield.

The ranking of cvs in terms of the rate of bulbing remains the same in different photoperiods. Hence, by comparing cvs in an extended photoperiod,

potentially suitable types can be quickly found as those that bulb at a similar rate to existing, locally adapted cvs (Mettananda and Fordham, 1997).

Sowing dates and bulb development

Bulb onions are grown from two major seasons of sowing – autumn for harvesting in the spring and early summer of the following year, and spring sowing for harvesting in the late summer of the same year. Figure 4.31 shows the seasonal pattern of leaf and bulb growth for typical spring- and autumn-sown crops. In many countries – for example, Israel, New Zealand and the UK – both autumn- and spring-sown crops are grown. In Israel sowings are made in all months between mid-September and late March, and bulbs are harvested between early March and late August. In this succession, cultivars with a progressively increasing photoperiod requirement for bulbing are sown, thereby ensuring there is always sufficient leaf growth before bulb initiation to produce large bulbs (Corgan and Kedar, 1990).

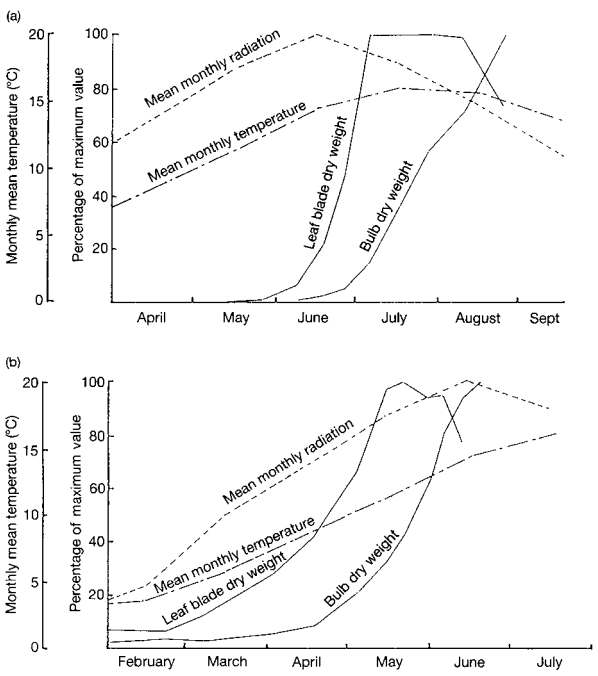

Fig. 4.31. The seasonal pattern of leaf and bulb growth of March-sown cv. 'Rijnsburger Bola' (a) and late August-sown cv. 'Senshyu Semi-globe Yellow' (b) onion crops at Wellesbourne, UK.

Crops sown in autumn develop bulbs in the following spring as photoperiods and temperatures increase. As Eqns 4.20 and 4.21 and Fig. 4.30 show, this means that the stimulus for bulbing – and, therefore, the rate of bulbing – increases as the season progresses. Spring-sown crops, especially in cool regions, develop bulbs well after midsummer, when photoperiod and mean temperature are decreasing. It follows from Eqn 4.20 that the rate of bulbing will then be declining with time. Furthermore, experiments show that onions will revert to leaf blade growth if they are transferred to sufficiently short days, even if they have reached an advanced stage of bulb development (see Fig. 4.28). Therefore, it is not surprising that, sometimes, bulbing fails to reach completion in spring-sown crops and they revert to leaf blade production, resulting in 'thick-necked' plants (see Fig. 6.11).

The role of red:far-red ratio in light in bulbing: effects of LAI

Table 4.1 shows that bulb maturity is advanced by higher-density planting and that this is associated with a high Leaf Area Index, LAI. Experiments show that any agronomic factor, like high plant density, early sowing or the use of 'starter' fertilizer (Brewster *et al.*, 1992 and Fig. 6.5), that tends to increase LAI will also accelerate bulb maturity date. Figure 4.32 shows the relationship between maturity date and percentage light interception by the leaf canopy for a range of cultivars. An early maturity date is the result of an early initiation of bulb scales.

Table 4.6 shows that neighbouring plants, which increase LAI and hence light interception by the leaf canopy, advance the date of bulb scale initiation. The relationships between rate of bulbing and photoperiod and temperature of Eqns 4.20 and 4.21 were derived from experiments on widely spaced plants where LAI was low, and this effect was not a complication. These relationships need to be modified by a 'leaf canopy effect' at higher LAIs (Mondal *et al.*, 1986c).

The onions recorded in Table 4.6 were grown hydroponically and supplied with complete nutrient solution, so competition for water or nutrients from

Table 4.6. The effects of shading by neighbouring plants on the mean day of the year of bulb scale initiation by onion cv. 'Prospero' grown hydroponically (from Brewster, 1990c, Table 7).

Treatment	Date of bulb scale initiation (day of the year)	Incident light intercepted (%) by the leaves	Red:far-red ratio (RFR) under leaves relative to value above leaves
Unshaded	230	14	0.94
Shaded by large onions	207	66	0.52
Shaded by carrots	202	61	0.40
SED (df = 4)	2.7	3.1	0.07

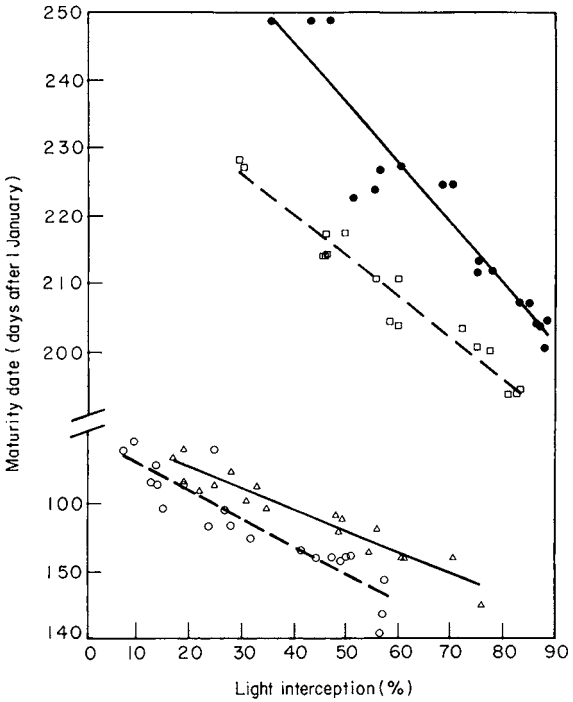

Fig. 4.32. Relationships between maturity date and the mean percentage of light (PAR) intercepted by onion crop leaves during bulbing. The lines are best-fitting linear regressions for cvs 'Express Yellow', ○ ; 'Keepwell', △ – both autumn-sown – and 'Augusta', □ ; and 'Robusta', ● – both spring-sown (from Mondal *et al.*, 1986a, courtesy of *Annals of Botany*).

neighbouring plants was not important. Furthermore, both large neighbouring onion and carrot plants elicited accelerated bulb initiation in the tested onions. This indicates that: (i) accelerated bulbing is associated with light competition, and not with factors in the root environment; and (ii) shading by any green foliage will accelerate bulb initiation. Table 4.6 also shows that the ratio of red to far-red wavelengths, i.e. 660:730 nm, in light under the denser leaf canopies is much reduced compared with daylight. Studies in controlled environments where onions have been grown under constant photoperiods and temperatures, but in light with a range of red:far-red ratios, show that the lower this ratio the faster the rate of bulbing (see Fig. 4.29b).

Many plant developmental processes, ranging from seed germination to stem elongation, are controlled by the red:far-red ratio in incident light. This ratio is lowered when light passes through leaf canopies, because leaves absorb red wavelengths more strongly than far-red. Therefore, this ratio is a sensitive indicator of the presence of leaves of neighbouring plants. The red:far-red ratio

in light is detected by the phytochrome pigment system. The main ecological significance of the phytochrome system seems to be the detection of the degree of shading experienced by a plant, or part of a plant, thereby enabling growth to be modified in an adaptive fashion (Smith, 1982).

In the case of onions, decreased red:far-red ratio in the incident light accelerates bulbing and crop maturity. Both increases in crop plant density and weed competition increase LAI and accelerate bulbing. It is not difficult to imagine that accelerated bulbing under competition from taller, faster-growing neighbours could have had survival value to the ancestors of onions. The low, slow-growing, weakly competive onions could bulb and enter a dormant phase when competition became intense, and could thereby survive until the following season.

It can be important that spring-sown crops reach an LAI at which this effect of decreased red:far-red ratio becomes significant. The resulting extra 'push' towards bulbing ensures that bulbs mature despite the decreases in photoperiod and temperature of late summer. Factors that decrease LAI – such as disease, pest or hail damage to foliage, low plant populations due to poor seedbed conditions, late sowing, damage from herbicides or stress from lack of nutrients or water during seedling growth – could all contribute to a failure of bulbing to reach completion, the reversion to leaf blade growth and thick-necked plants (see Fig. 6.11). This will particularly be the case in cool summers, when the rate of bulbing is slowed by low temperature (see Eqn 4.21).

Studies in which bulb-inducing photoperiods were interrupted by 3 h of light of a specific wavelength have produced an 'action spectrum' for onion bulbing showing that the most effective wavelength is 714 nm, i.e. just beyond the visible red in the far-red region of the spectrum. The promotive effect of a period of far-red light can be reversed by following it immediately with red light, confirming the involvement of phytochrome (Lercari, 1983). The bulb-promoting effect of a period of far-red light is maximal if it occurs near the middle of the photoperiod. The importance of the timing of such treatments relative to the 24 h cycle of light and dark suggests that daily (circadian) rhythms are involved in the phytochrome response. Circadian rhythms are implicated in many plant photoperiodic responses (Thomas and Vince-Prue, 1996). The photoperiodic, red:far-red and temperature responses of bulbing may all be interrelated via some, as yet unknown, common control system that involves phytochrome.

Plant and leaf age effects

Experiments in which plants of different ages were defoliated to a similar leaf area and then transferred to bulb-inductive photoperiods showed the older plants bulbing more rapidly than the younger ones. On the other hand, removal of either young leaves or old leaves on plants of the same age, and then

transfer to inductive photoperiods, showed the younger leaves to be more effective in inducing bulbing (Sobeih and Wright, 1986).

The increased time required for bulbs to initiate as photoperiods decrease has been interpreted as evidence for a progressively decreasing 'critical' photoperiod needed for bulbing as plants age (Wiles, 1989). This is an alternative interpretation of data such as those in Fig. 4.30 in invoking a slower *rate* of bulb initiation at shorter photoperiods, as implied by Eqns 4.20 and 4.21. It has yet to be shown conclusively which of these interpretations is correct, or whether they are both partly true.

Pre-planting storage temperature and the bulbing of sets

If onions are grown from sets, there are numerous reports (e.g. Aura, 1963; Brewster, 1990a) that storage of sets at 28–30°C for several months prior to planting results in bulbing and maturity up to 1 month later than in sets stored at 20°C or below. The consequent longer growing season allows more time for leaf growth and gives higher yields. In shallots and multiplier onions also, storage at 28–30°C – or in some strains 20°C – before planting delays maturity, prolongs the growing season and increases yields. Therefore, when growing onions and shallots from bulbs rather than seeds, the timing of leaf growth and bulb development is influenced by storage temperatures prior to planting, as well as by temperatures and photoperiods while the crop is growing in the field.

Figure 4.33 summarizes the environmental control of bulbing in onion and indicates how factors interrelate.

The biochemistry of onion bulbing

When onion plants are transferred from non- to bulb-inducing conditions, a rise in reducing sugar, sucrose and fructan (see Chapter 8, 'Carbohydrate Biochemistry') concentrations occur in the sheath (pseudostem) tissue within 5–10 days. Reducing sugar concentrations in the leaf blades also increase. At the same time, a rapid decrease has been measured in the level of a soluble acid invertase, an enzyme that catalyses the conversion of sucrose to the reducing sugars glucose and fructose. These changes occur before visible bulb swelling (Lercari, 1982a, b).

Bulb swelling may involve the hydrolysis of previously accumulated fructans to fructose and glucose (Darbyshire and Steer, 1990). This could increase the osmotically active solutes in the outer sheath cells, thereby drawing in water and driving cell expansion. A swelling of leaf sheaths and the cessation of leaf blade development, along with bulbing ratios of three or more, have been induced in non-inductive photoperiods in onion plants growing *in vitro* on agar containing tissue culture nutrients when the sucrose concentration in the medium was

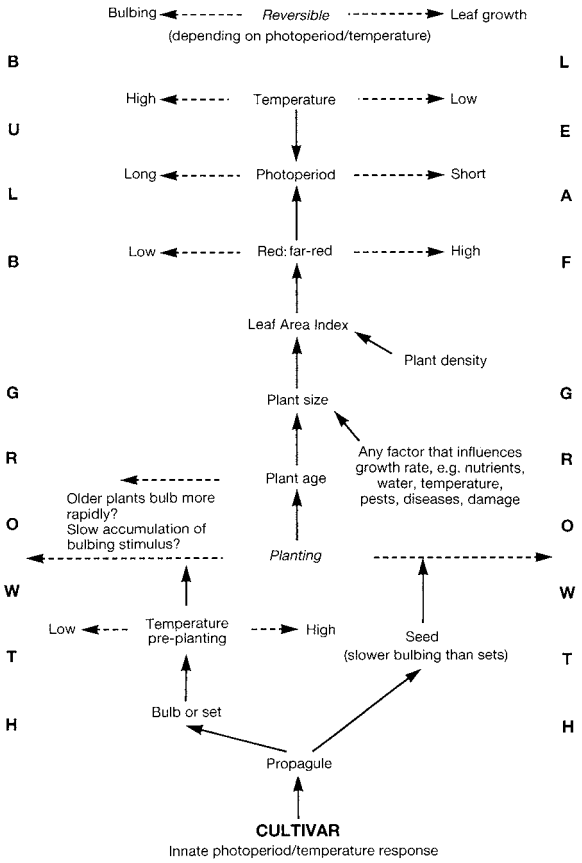

Fig. 4.33. A schema showing the main factors that control bulbing in onions and how they interrelate.

raised from 40 to 120 g/l (Kahane *et al.*, 1992). However, bulb scales did not form and there was no reduction in cell division or development of dormancy at the centre of the 'bulb'. A similar increase in bulbing ratio, along with an accumulation of soluble carbohydrates, is induced by nitrogen deficiency in onions in non-inductive photoperiods (Brewster and Butler, 1989).

Attempts to isolate a 'hormone' responsible for bulbing have not been successful, but auxin, cytokinin, gibberellins and ethylene have all been implicated in bulbing. Externally applied ethylene (released from sprays of 'ethephon') induces a swelling of leaf sheaths and some increase in bulbing ratio, but the elongation of sheaths that normally accompanies bulb swelling does not occur. Consequently, the appearance of ethylene-treated plants is not typical of normal bulbing. Furthermore, although leaf bases swell as a result of ethephon treatment, the bladeless bulb scales typical of normal bulbing do not develop (Sobeih and

Wright, 1987). In addition, ethylene antagonists do not prevent bulbing in inductive photoperiods. The increases in bulbing ratio caused by ethylene or by high sugar levels do not result in dormant bulbs with bulb scales, and hence this should be regarded as 'pseudobulbing' rather than true bulbing.

Several studies implicate gibberellins in onion bulbing. An inhibitor of gibberellin biosynthesis, coded S-3307, promotes bulbing in non-inductive photoperiods. It also causes microtubules in the cells of onion leaf sheaths to orientate longitudinally, whereas gibberellin application causes transverse orientation (Mita and Shibaoka, 1984). The orientation of microtubules determines the orientation of the cellulose microfibrils that reinforce cell walls. Bulb-inductive photoperiods cause microfibrils to lose the transverse orientation found in non-inductive conditions. Therefore, changes in the architecture of the cellulose reinforcement of sheath cell wells are associated with bulbing, and these changes can be mimicked by the gibberellin antagonistic S-3307. Shallot plants growing in the *in vitro* system mentioned above could be prevented from bulbing in inductive photoperiods by inclusion of 10 μM GA_3 in the culture medium. Inclusion of the anti-gibberellin ancymidol in the medium increased bulb swelling but did not induce normal, complete bulbing in non-inductive photoperiods (Le Guen-Le Saos *et al.*, 2002).

MODELS FOR ONION GROWTH AND BULBING

Various approaches have been taken in developing models to predict onion growth and/or development. Lancaster *et al.* (1996) used field data on the growth and bulb development of cvs 'Pukekohe Long Keeper' and 'Early Long Keeper' grown from a wide range of sowing dates in two regions in New Zealand to develop an empirical model to predict the photoperiods and temperatures needed for bulbing and the date and bulb size at maturity. For bulbing to start, a minimum photoperiod of 13.75 h and a thermal time (T_b = 5°C) since sowing > 600°C days were required. The bulb size at maturity could be predicted from the bulb diameter at the start of bulbing, d_B, and the number of leaves appearing after bulbing, n_L: d_B depended on the thermal time from sowing to bulbing and n_L was a function of the date bulbing started. A similar model could be useful for other cvs in other localities, but it would need to be developed using local field data.

Scaife *et al.* (1996) fitted a range of equations containing biologically meaningful parameters to the growth in dry weight of a bulb onion crop in central England. They found that the best fit to the data with no indication of systematic deviations was given by an 'expolinear' equation using accumulated 'effective day-degrees (EDD)' (Eqn 4.19) rather than time or day-degrees as the independent variable. This equation models the growth of mutually shading plants in a crop as they pass from the exponential growth phase of spaced seedlings to linear growth in crop dry weight when the leaf canopy is closed.

The equation is:

$$\ln w = \ln mx + \ln \ln[kL_0 + \exp(-rx)] \quad \text{(Eqn 4.22)}$$

where the symbols and the values derived from fitting the model and the units are:

w = crop dry weight, g/m^2

x = EDD from the first sampling; the base temperature for EDD was 5.9°C and the light response term f, was 0.136 $MJ/m^2/°C$ day (Brewster and Sutherland, 1993)

m = maximum crop growth rate = 2.92 (g/m^2/EDD)

k = light extinction coefficient = 0.43

L_0 = initial leaf area index (a measured input)

r = initial relative growth rate = 0.0200 (per EDD)

This equation provides a simple description of onion crop growth rate, which varies according to changing temperature and light income. The equation has general validity since it is based on crop physiological theories. Modification to incorporate some 'optimum temperature' above which EDDs no longer increased as temperature increased would probably be needed to apply this approach in warm climates. The model provides no information about development, just the dry weight growth of a well-adapted cultivar.

A comprehensive mechanistic simulation model of bulb onion crop growth and development, called 'ALCEPAS', has been developed by de Visser (1994a, b). This utilizes the general crop growth simulation model SUCROS87 (Spitters *et al.*, 1989) and combines it with a model for onion development rate from seedling, through bulbing to ripening and senescence. Figure 4.34 shows the relational diagram of ALCEPAS; the continuous lines represent flows of dry matter entering the various material fractions of the crop, e.g. root or bulb + neck, represented by oblong boxes, and the broken lines represent flows of information that influence the rate processes in the 'valve' symbol boxes. The rate processes are determined by equations, the numerical inputs to which depend on the values of the variables shown as information flows (broken lines).

The Developmental Stage (DVS) between emergence and bulbing was predicted using equations based on the relationships illustrated in Fig. 4.30 and Equation 4.21, modified by a factor to account for the R:FR effect that depends on LAI, as discussed in a previous section. DVS from bulbing to ripening was simply a function of thermal time with 6°C base temperature. An equation of general applicability to crops, based on the proportion of protein and mineral ash in a tissue, was used to predict maintenance respiration rate. A similar equation based on the proportion of carbon and ash in a tissue was used to predict growth respiration. Material from field experiments was analysed to determine ash, carbon and protein contents of roots, shoots and bulbs and how they changed with developmental stage.

Field experiments provided data for: (i) equations for specific leaf area (SLA), and how it varied with developmental stage and plant density; (ii)

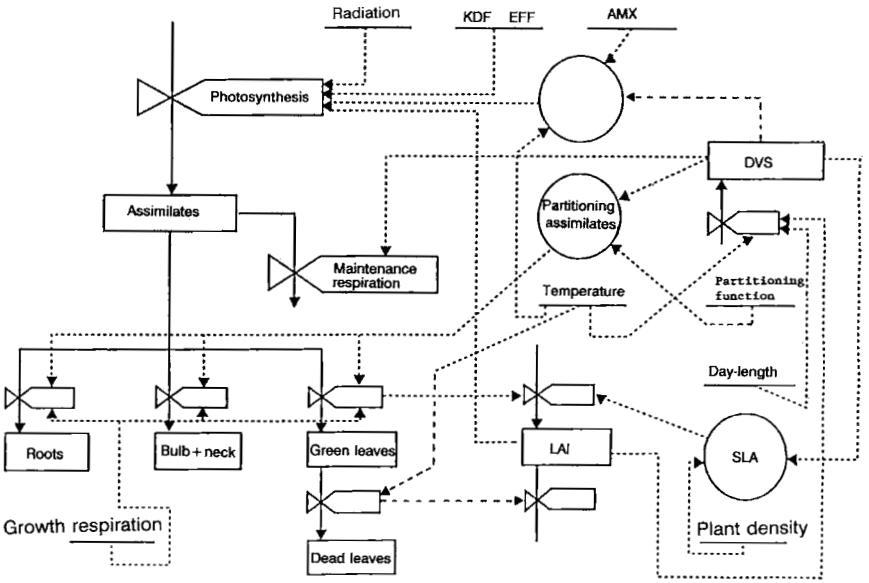

Fig. 4.34. Relational diagram for the onion growth and development simulation model ALCEPAS, based on the general crop growth simulation model SUCROS87. AMX, gross assimilation rate at light (PAR) saturation of an individual leaf (kg/ha/h); DVS, development stage of bulb onion crop (50% emergence = 0; 50% bulbing = 1; leaf fall (maturity) = 2); EFF, maximum PAR use efficiency of a leaf (kg/J (i.e. at low PAR)); KDF, extinction coefficient for PAR in leaf canopy; LAI, leaf area index; SLA, specific leaf area (cm^2/g) (from de Visser, 1994a. Courtesy of *Journal of Horticultural Science and Biotechnology*).

equations for the longevity of leaves and its variation with temperature; (iii) KDF, the PAR extinction coefficient of the leaf canopy (Eqn 4.2); and (iv) an equation describing how the partition of new growth between leaves and bulbs changes with developmental stage (the graph of this function was of the same form as in Fig. 4.27).

A function to describe how partition of new growth to roots changed with developmental stage was derived from published work. The photosynthesis parameters: (i) AMX, the PAR saturated assimilation rate of a leaf; (ii) EFF, the PAR use efficiency of a leaf at low PAR; and (iii) the scattering coefficient of leaves for PAR were not measured or known, but were found by running the model with growth data from field experiments and optimizing for the values of these parameters. The optimized values were close to those previously used in SUCROS87 for spring wheat (Spitters *et al.*, 1989).

ALCEPAS combines the determinants of crop growth and yield outlined at the beginning of this chapter, encapsulated in SUCROS87, with a model incorporating much of the information described above that is particular to the

control of development in bulb onions. It therefore provides a powerful conceptual framework for understanding the bulb onion crop and seeing how many factors interrelate to influence yields and maturity date. With modification of the functions relating bulb development rate to photoperiod, it could probably be made applicable to other cvs growing in climatic zones different from north-western Europe.

The simulation model proved reasonably successful at predicting growth and bulb development on fertile soils in the Netherlands, where it was developed. There is no provision for the effects of nutrient and water stress in the model, and overestimates of yield in some model validation trials indicated previously undetected influences of such stress at some sites (de Visser, 1994b). Such a growth model could be combined with simulations for disease development (see Chapter 5) to make assessments of likely disease impact on yields.

PHYSIOLOGY AND ENVIRONMENTAL CONTROL OF FLOWERING

Flowering is an essential prerequisite of seed production, and its importance is self-evident for all but the purely vegetatively propagated alliums. When producing bulbs or growing shoots for food, flowering is generally unwanted, except in the unusual case of Chinese chives, in which both inflorescences and leaves are eaten. Apart from this, flowering or bolting downgrades the quality of the crop and may curtail the growing season, for example in leeks or salad onions. Therefore, an understanding of flowering, and how it interacts with vegetative growth and bulbing, is important for successful food crop production as well as for seed production. Flowering has been most fully investigated and is best understood in onion. Research on flowering in onion has been reviewed by Brewster (1997a,b) and Rabinowitch (1990a), pollination by Currah (1990) and seed development by Rabinowitch (1990b), and fuller reference lists can be found there.

Onion flowering

The sequence of stages in floral development

Stages in inflorescence initiation and development are shown in Figs 2.6 and 2.17. The sequence of stages in the cycle from seed germination to seed ripening in the life cycle of an onion is illustrated in Fig. 4.35. Each stage of this cycle has different environmental requirements. For some stages, different cultivars are known to have different environmental optima, and to require different lengths of time to pass through the stage. Also, when inflorescences develop within bulbs, the rate of initiation is strongly influenced by the size of the bulbs. Some stages in the life cycle progression can be reversed; for instance, 'devernalization' can

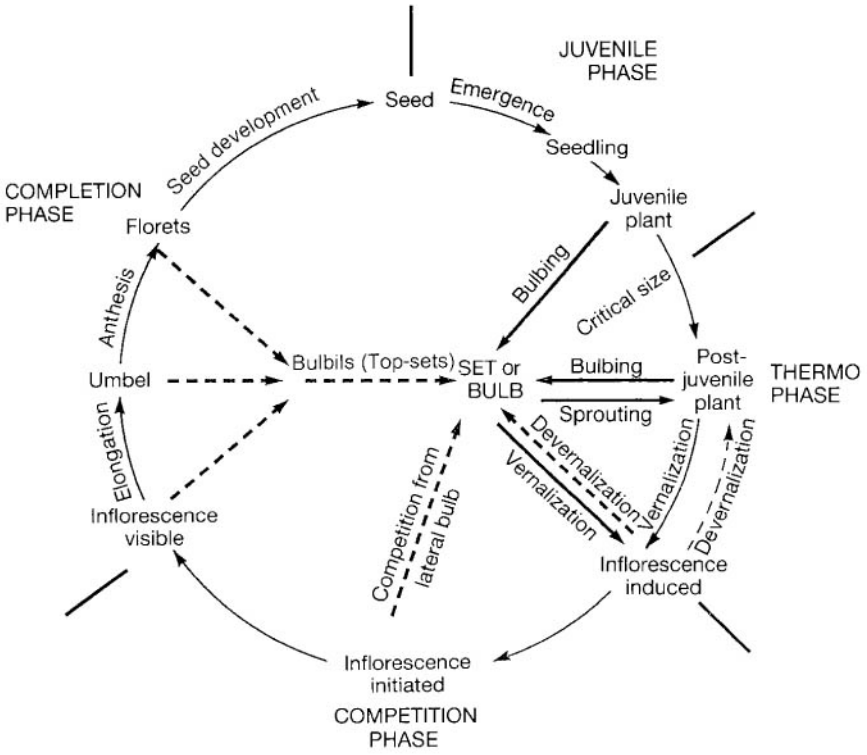

Fig. 4.35. Stages in the life cycle of onion plants with particular reference to flowering. Unusual or reversionary developmental processes are shown by broken lines.

nullify inflorescence induction. Processes occurring at the shoot apex within bulbs can be observed only by destructive sampling, so progress in these phases is difficult to assess.

Because of: (i) the changing environmental needs of different phases in the sequence; (ii) differences in the rate of progress through each phase, depending on cultivar and bulb size; and (iii) the possibility of reversion or deviation from the normal pathway of development at various points along the route, reports of the effects of environmental factors on flowering may give apparently contradictory results, and it is difficult to predict the outcome of a particular combination of agronomic conditions on flowering. Nevertheless, a clear general pattern of environmental requirements for each stage in the cycle of Fig. 4.35 is known, even though quantitative information is limited to that from experiments on a few cultivars at each stage. Therefore, given careful experimentation with sufficiently detailed observation, it is possible to understand flowering behaviour in field conditions even if it cannot yet be predicted without experimentation.

The stages described in Fig. 4.35 can be grouped into four broad phases: (i) 'Juvenile phase'; (ii) 'Thermo phase'; (iii) 'Competition phase'; and (iv) 'Completion phase' (van Kampen, 1970). The stages within each phase have similar environmental requirements, but different phases have different requirements. During the juvenile phase onions cannot be induced to flower; they must reach a certain critical weight or leaf number before they can enter the thermo phase, in which they can be induced by low temperatures to initiate inflorescences. Inflorescence initials, once formed, can be destroyed and are observed to wither and degenerate in conditions that favour bulb development. This is termed the 'competition phase', because of the apparent competition between inflorescence development and bulb development. Inflorescences are particularly vulnerable before they are visible outside the bulb or pseudostem. Once inflorescences are visible, the completion phase is favoured by higher temperatures than the previous two phases. Temperature ranges and optima for the mostly temperate region cultivars so far investigated, and other important environmental influences at each phase, are outlined in Table 4.7.

The minimum size for flower initiation

The critical plant size above which inflorescence induction can occur depends on cultivar. For example, seedlings of the Dutch spring-sown cv. 'Rijnsburger' can be induced when they have seven or more leaves initiated (counting the cotyledon as one), whereas the more bolting-resistant, autumn-sown cv. 'Senshyu Semi-globe Yellow' must have ten or more leaves initiated. Shoot dry weights of 0.06 and 0.45 g correspond to these two leaf stages, respectively. The transition from a zero to a maximum inflorescence initiation rate occurs over a narrow weight range in seedlings (see Fig. 4.36).

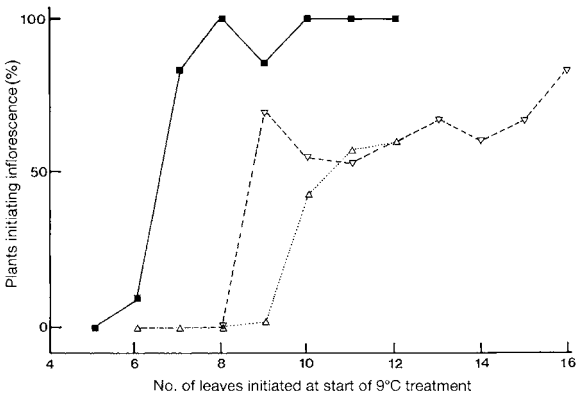

Fig. 4.36. The effect of the number of leaves initiated at the start of vernalization on the proportion of plants with inflorescence initials after 77 days at 9°C and 18 h photoperiods for cv. 'Rijnsburger Bola' (solid squares, spring-sown cv.) and cv. 'Senshyu Semi-globe Yellow' (open triangles, autumn-sown cv.) (from Brewster, 1985. Courtesy of *Annals of Botany*).

Table 4.7. Temperature requirements (°C) and other important factors for the various phases of the life cycle of onions relevant to inflorescence development.

Stage of development (phase)	Optimum	Range	Other important factors
Germination (juvenile)	25	0–37	Water, aeration
Emergence (juvenile)	20–25	3–37 (13–28 for > 70% emergence)	Water, aeration
Vegetative growth (juvenile)	20–25	10–35	Light, water, nutrients, photoperiods shorter than for bulbing
Vernalization (thermo)	7–12	2–17	In growing plant: low N, high soluble carbohydrate, long photoperiod
Inflorescence development within bulb or plant (competition)	15–17	10–18	In growing plant: normal N (3.0–3.5% dm), long photoperiod
Scape elongation (completion)	25–35	15–40	
Anthesis (completion)	25–35	15–35	Florets open in daylight
Pollination (completion)	27	15–43	RH < 70% increases pollen shedding
Seed development (completion)	25–30	15–43	50°C is lethal
Reversionary or deviant development			
Devernalization	28–31	21–35	
Inflorescence degeneration within plant by competition from bulbing	25–30	?	Long photoperiod plus high temp; sudden transfer from cool to warm (e.g. 14 to 27°C)
Bulbil formation in inflorescence	31	?	Induced by removal of florets and water or kinetin sprays
Leaf blade-like structures from spathe or inflorescence	?	?	Short photoperiods while inflorescence develops

By contrast, in bulbs there is a wide range of size or weight over which the rate of inflorescence initiation increases with size. For example, in the Japanese cv. 'Sapporiki', 50 g (fresh weight) bulbs could be induced to 50% flowering by 20–30 days exposure to 9°C but 5 g bulbs need more than 80 days. As a consequence, larger bulbs complete the thermo and competition phases of inflorescence development before smaller bulbs. This is why small bulbs (sets) are used for vegetative propagation where flowering is not wanted.

Similarly to seedlings, spring-sown cultivars can be induced to flower as smaller bulbs than the more bolting-resistant, autumn-sown cultivars. The spring-sown cv. 'Sapporiki' initiates inflorescences at half its maximal rate in bulbs of 14 g fresh weight, whereas the autumn-sown cv. 'Senshuki' has to be about 28 g. In cv. 'Sapporiki', inflorescence initiation reaches its maximum rate in bulbs of 50 g weight and in cv. 'Senshuki' in bulbs of 100–150 g. Studies on the British spring-sown cv. 'Ailsa Craig' indicate an absolute minimum bulb weight for inflorescence development of about 4 g; this would represent a dry weight of 0.40–0.50 g, considerably heavier than the 0.06 g minimum dry weight needed for seedlings of cv. 'Rijnsburger', indicating that the minimum critical dry weights of bulbs (sets) are seven or eight times higher than for seedlings (Brewster, 1987).

Environmental control of inflorescence initiation and development

Temperatures needed for inflorescence initiation have been studied in a number of temperate region cultivars and, from the combined results, the relationship shown in Fig. 4.37 was derived. Optimum temperatures in this thermo phase are 8–12°C, and vernalization is definitely slower at 6°C or less. The optimum temperature is higher than the optimum of about 5°C for vernalization in most temperate vegetables (Wiebe, 1990).

The optimum temperature for onion vernalization varies with cultivar; the West African cv. 'Bawku' is optimally induced at 15–21°C, whereas strains from northern Russia have an optimum of 3 to 4°C. The time required for vernalization may also vary with cultivar; for example, seedlings of the Japanese spring-sown cvs 'Sapporiki' and 'Imai-wase' can be 50% induced by just 20 days at 9°C, whereas the autumn-sown 'Senshuki' requires 30–40 days.

Temperatures of 28–31°C applied to bulbs previously induced by low temperatures can reverse inflorescence induction, and this is termed 'devernalization'. The duration of storage at 28–31°C needed to prevent flowering increases the more advanced the stage inflorescence initiation. This is illustrated by the results of Aura (1963) on Finnish cultivars. In accord with the results discussed above, he found that inflorescence initiation was more rapid in bulbs stored at 9–13°C than at 3–5°C and that it was more rapid in large bulbs than in small ones. Reflecting these differences, in a total storage period of 8 months a terminating duration of 5 months at 28°C was needed to suppress flowering in bulbs stored at 9–13°C, but only 2 months in those stored at 3–5°C. Also, the duration of 28°C treatment needed to suppress flowering in 15 g bulbs was less than needed for 108 g bulbs.

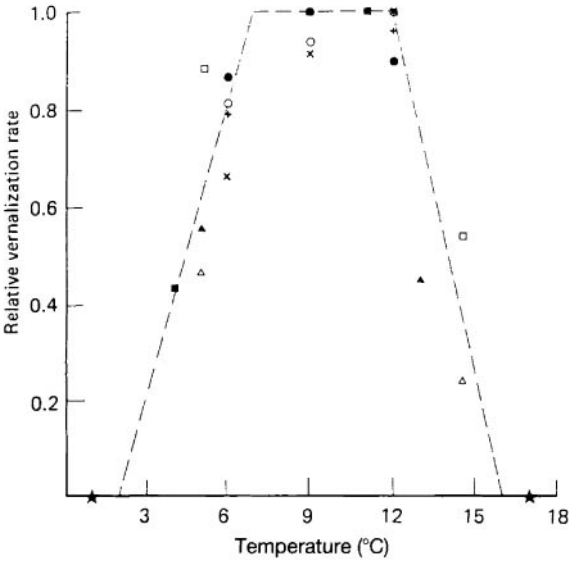

Fig. 4.37. The relative rate of vernalization *versus* temperature for European and Japanese cvs of onion. Different symbols indicate results from different series of experiments (from Brewster, 1987).

When an inflorescence initial has developed within a bulb to stage 4 of Fig. 2.6, its subsequent rate of elongation depends on temperature and, after the bulb has sprouted and started to grow, on day-length. Long photoperiods coupled with fairly cool temperatures (10–15°C) are optimal. A vegetative shoot apex normally develops axillary to the inflorescence (see Fig. 2.6), and this can develop more rapidly than the inflorescence under a combination of warm temperatures (20°C or higher) and long photoperiods (e.g. 16 h, although this probably depends on cultivar). This results in the swelling of the axillary bud to form bulb scales and the shrivelling and degeneration of the young scape (see Fig. 4.38), hence the term 'competition phase' coined by van Kampen (1970) to describe the apparent competition between axillary bud and inflorescence. When onions are planted out in bulb-inducing conditions – for example, in a warm spring or in a glasshouse in spring – such inflorescence abortion can be common, even from bulbs with advanced inflorescence initials.

As discussed under bulbing, bulb or set storage at 28–30°C also delays bulb initiation. Because bulb development suppresses inflorescence elongation during the competition phase, a short period (1–2 months) of storage at such a high temperature at the end of a long period of cool storage can, by delaying bulbing, actually result in increased bolting (see Fig. 4.39), although longer periods at high temperature do suppress flower initiation and bolting.

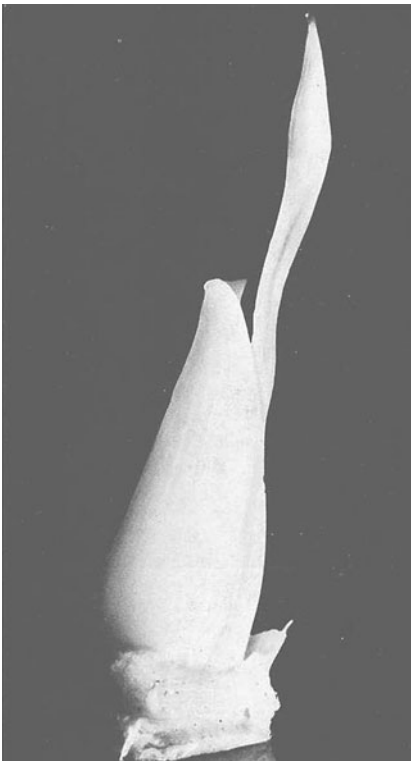

Fig. 4.38. Inflorescence abortion caused by 'competition' from bulbing with characteristic shrivelling of the flower stalk just below the spathe (from van Kampen, 1970. Courtesy of *Mededeling Proefstation voor de Groenteteelt in de Vollegrond, Lelystad*).

Inflorescence initiation in growing seedlings is influenced by photoperiods, nitrogen nutrition and daily radiant exposure as well as by temperature. Long photoperiods increase the rate of inflorescence initiation, but a low nitrogen status can largely replace the requirement for long photoperiods (see Fig. 4.40). Exposure of seedlings to low light intensities prior to vernalization, resulting in a low concentration of non-structural carbohydrates in the plants, slows subsequent inflorescence initiation and increases the critical leaf number needed to reach the post-juvenile stage by one or two leaves.

Once inflorescences are first initiated within seedlings, subsequent development through to stage 4 (see Fig. 2.6) and further elongation tends to be faster as temperature increases in the range 6–12°C, faster with longer photoperiods at these cool temperatures and faster in high-, rather than low-, nitrogen status plants. Temperatures of 12–16°C in combination with photoperiods of 16–17 h have been found satisfactory for inflorescence emergence

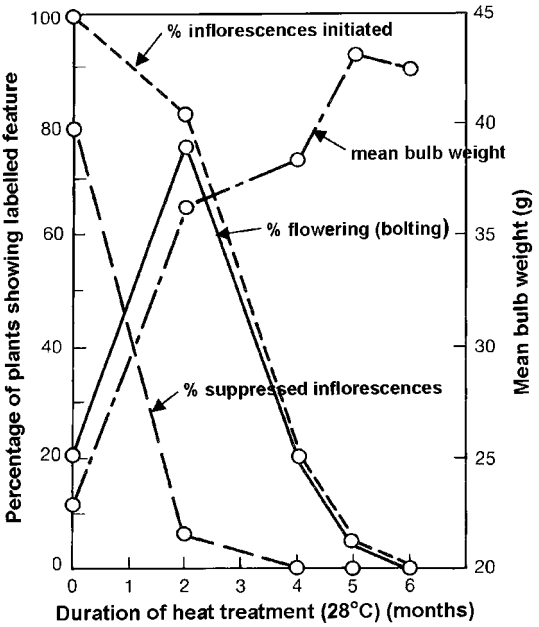

Fig. 4.39. Effect of duration of heat treatment of bulbs at 28°C during storage pre-planting on flowering and bulb yield in the following season in onion cv. 'Juva 1' in Finland. Percentage of plants with: (a) visible inflorescences (unbroken line), (b) inflorescences initiated (short broken line), (c) suppressed inflorescence initials (long broken line) and (d) average weight of bulbs at harvest (alternate short and long broken line) (from Aura, 1963. Courtesy *Annales Agriculturae Fenniae*).

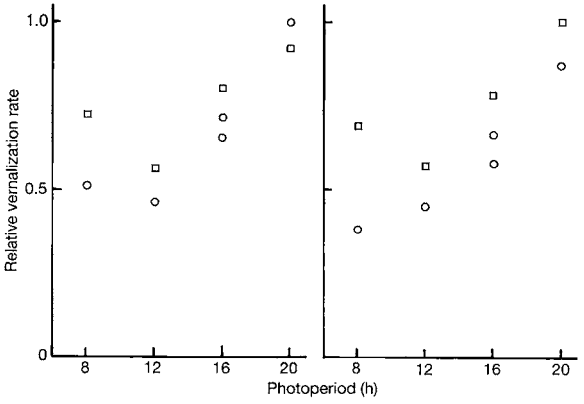

Fig. 4.40. Influence of photoperiod on vernalization rate at 9°C of onions grown with abundant N (○) or deficient in N (□). Left-hand graph, the autumn-sown cv. 'Senshyu Semi-globe Yellow'; right-hand graph, the spring-sown cv. 'Rijnsburger Bola' (from Brewster, 1983).

from induced bulbs and plants of intermediate-day cultivars. Since the photoperiods and temperatures needed for bulbing vary with cultivar, it is almost certain that the photoperiods and temperatures needed to avoid suppression of developing inflorescences by competition from bulbing will depend on cultivar. The inflorescence of a short-day cultivar will be suppressed by a shorter day-length than a long-day cultivar. Also, plants raised from bulbs or sets bulb more rapidly than those raised from seeds (Fig. 4.33), unless they have been 'heat treated' at the end of storage (see Fig. 4.39), and therefore competition from bulbing probably suppresses inflorescences in bulb-raised plants at shorter photoperiods and lower temperatures than in seed-raised plants.

Abnormal inflorescences: bulbils and leafy shoots in the umbel

Quite frequently small bulbs, known as 'bulbils' or 'top-sets', may form in the inflorescence rather than normal flowers and seed capsules (see Fig. 4.41). When this occurs the scape is shorter than normal. Various degrees of this condition have been observed, ranging from the production of a single, large 'bulbil' on an extremely short scape through to near-normal inflorescences with a mixture of normal seed capsules and bulbils. Sometimes, when this occurs, the spathe elongates and turns green so as to resemble a leaf blade; sometimes the bulbils themselves develop to produce secondary inflorescences bearing normal flowers.

Studies on Finnish cultivars showed that the production of bulbils was promoted by storage for 6 weeks at 28°C, or better 31°C, following an

Fig. 4.41. Bulbils, or 'top-sets', formed on an onion inflorescence (photograph courtesy of Warwick HRI).

inflorescence-inducing cold treatment of 5–6 months. As described above, high-temperature bulb storage (28–31°C) can cause growing points at a critical stage of inflorescence initiation to revert to the vegetative state and to form leaf initials. If the inflorescence has already developed to a certain extent at the start of such a heat treatment the meristem may be diverted to bulbil development. Such a meristem in the early stages of inflorescence differentiation will probably produce one bulbil on a short scape whereas, if the heat treatment occurs late in inflorescence development, a mixture of bulbils and normal florets may develop. Therefore, the stage of inflorescence development reached by the apex at the start of heat treatment probably determines the outcome.

The 'top' or 'tree' onion (see Chapter 1, 'Cultivated Hybrids of *Allium cepa*'), represents an extreme condition in which large bulbils are always produced in inflorescence-like structures, and normal flowers do not occur. Bulbils can be induced to form in normal inflorescences by clipping off the developing florets. Such bulbil production can be increased by spraying the clipped heads with water, or better, benzyl adenine solution.

Another deviation from normal inflorescence development has been observed when induced plants have been allowed to develop inflorescences in abnormally short photoperiods, for example 8–10 h. Under these conditions inflorescence appearance is slow, scapes are short and spathes may become long, green, curved and leaf-like (Scully *et al.*, 1945), or several leafy vegetative shoots may occur in the inflorescence (van Kampen, 1970).

The completion phase, flower opening and pollination

Once a spathe is visible the plant enters the 'completion phase' of the flowering process. Here, higher temperatures become optimal. About 400°C days > 10°C are required to progress from spathe appearance to peak flowering, and 900°C days > 10°C to reach a stage where ripe seeds begin to shed from seed capsules (Brewster, 1982). Scapes normally elongate to a length of 1–2 m. Individual bulbs may produce between one and 20 inflorescences depending on genotype, bulb size and environmental conditions; three to six inflorescences is common. The spathe opens to produce a roughly spherical umbel containing between 50 and 2000 individual flowers, although 200–600 is the normal range. There is no very regular sequence of flower opening on an umbel. The most strongly insolated parts of the umbel tend to produce open florets first, and there is a general tendency for upper florets on the umbel to precede the lower ones in opening. The pedicels of later-opening florets elongate to carry them clear of earlier-opening, maturing florets.

The sequence of individual flower development consists of petal opening (anthesis) coinciding with the start of nectar secretion, the dehiscence of the inner whorl of anthers, and then the outer whorl. Meanwhile, the style elongates from 1–2 to 5–6 mm and develops a sticky stigma knob after the anthers have dehisced. Then nectar secretion ceases and petals, stamens and style start to wither. The whole process takes 10 days at 18°C or 5 days at 30°C. The greatest

seed set, best embryo development and most rapid pollen tube growth occurred at 35/18 (day/night °C) (25°C mean) (Chang and Struckmeyer, 1976a, b). Air relative humidity < 70% accelerates pollen shedding by anthers.

The ovary in each flower contains six ovules, and about half the pollen tubes at the top of a stigma grow as far as the ovary; therefore, 12 or more initial pollen tubes are needed to achieve maximum seed set. In fact, the production of three to four ripe seeds per ovary is common in good seed crops.

Nectaries, easily accessible to many types of pollinating insect, are located between the base of the ovary and the flattened, widened base of the inner whorl of stamen filaments. The nectar is primarily a hexose sugar solution and it fluoresces with ultra-violet light that is visible to insects (see also Chapter 6, 'Seed Production').

Fertilization and seed development

Following pollination, fertilization of ovules starts within 12 h and is complete in 3–4 days. Pollination itself stimulates the initial development of ovules and ovaries. The shrinkage and loss of green colour in unfertilized ovaries does not occur until about 3 weeks after flowering, making the early assessment of seed-set difficult.

In fertilized ovules the endosperm nuclei start to divide first, and cell division and expansion by the embryo occurs 5–6 days later. The embryo develops from a globular, few-celled pro-embryo, which is first visible in microscope sections about 6 days after pollination. It then develops through an oval to tubular, and finally to a coiled tubular structure embedded within the endosperm. The embryo reaches its full development when the seed attains maximum dry weight (see Fig. 2.19). Initially the endosperm is liquid, and this is termed the 'milk stage'. At about 17 days or 330 DD (degree-days above 0°C) after pollination, cell walls develop within the endosperm and it progresses to the pasty 'dough stage' at about 24 days or 450 DD after flowering. At this point the seedcoat starts to turn black. The seed attains its maximum fresh weight at about 30 days or 570 DD after flowering.

Up to this point seed dry weight growth is near exponential and seed dry weight is then about half its maximum. The endosperm then becomes solid and the seed reaches its maximum dry weight, typically 3.0–3.5 mg, at 810 DD after flowering, normally about 45 days after flowering (Gray and Ward, 1987). At this stage capsules begin to shatter and to shed seed (see Fig. 6.17), and the food-reserve oil globules and protein bodies can first be seen within seeds. Seed water content declines after the attainment of maximum fresh weight. Germinability commences just before the maximum fresh weight is attained (570 DD after flowering) and is near maximum at seed shatter.

INTERRELATIONS OF GROWTH, FLOWERING AND BULBING IN ONION

Figure 4.42 summarizes how growth, bulbing and flowering are controlled by temperature and light conditions. Advances in understanding of crop behaviour should become possible by combining models for these processes. Predictions of how bolting, bulb yields and maturity date are affected by sowing date, locality and season can be compared with field experiments, to ascertain whether the models are satisfactory.

For example, the photothermal bulbing model (Eqn 4.20) predicts that widely spaced cv. 'Keepwell' will initiate bulb scales on 31 May when grown as an overwintered crop in a year with average temperatures at Wellesbourne, UK. Cv. 'Keepwell' is very similar to cv. 'Senshyu' in its date of bulbing and maturity (NIAB, 1982) and similar in bolting response. A model for inflorescence formation, based on the vernalization responses described above (Brewster, 1997b), with inputs of daily temperature and photoperiod, indicated that some sowings of overwintered 'Senshyu' crops would reach the stage of spathe in-

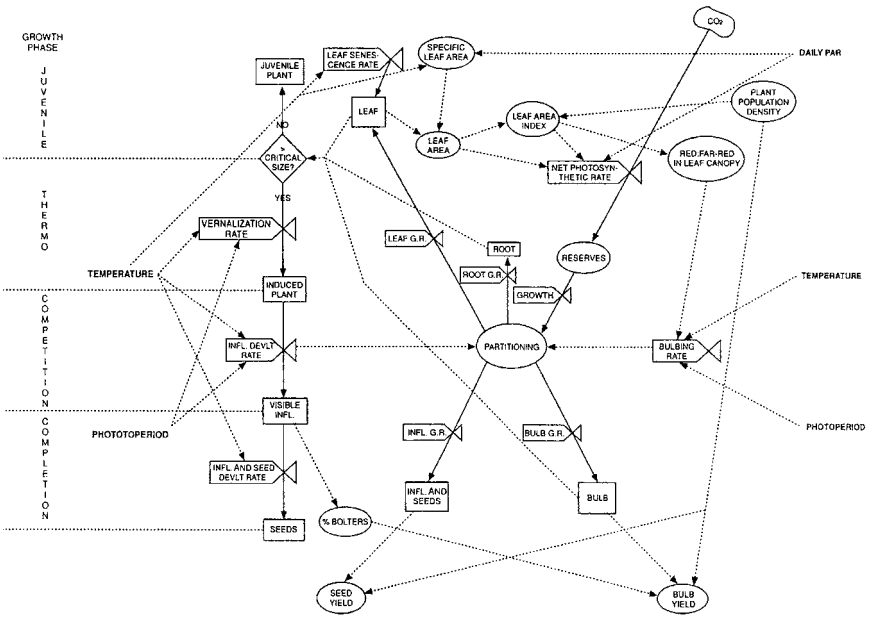

Fig. 4.42. A relational diagram indicating the main environmental controls of growth and development in onions, showing how growth, bulbing and flowering interrelate to determine bulb or seed yield. Progress through the growth phases of Fig. 4.35 is indicated on the left of the diagram. Devlt, development; Infl., inflorescence; G.R., growth rate (dry matter growth); PAR, photosynthetically active radiation.

itiation well before 31 May (see Fig. 4.43). Such crops are likely to bolt because scape elongation will occur before competition from bulbing begins to suppress developing inflorescences. Small intervals between sowing dates translate into much longer intervals between the dates at which plants reach the various stages of inflorescence development, depending on how temperatures vary over the autumn, winter and spring – which, of course, varies from year to year.

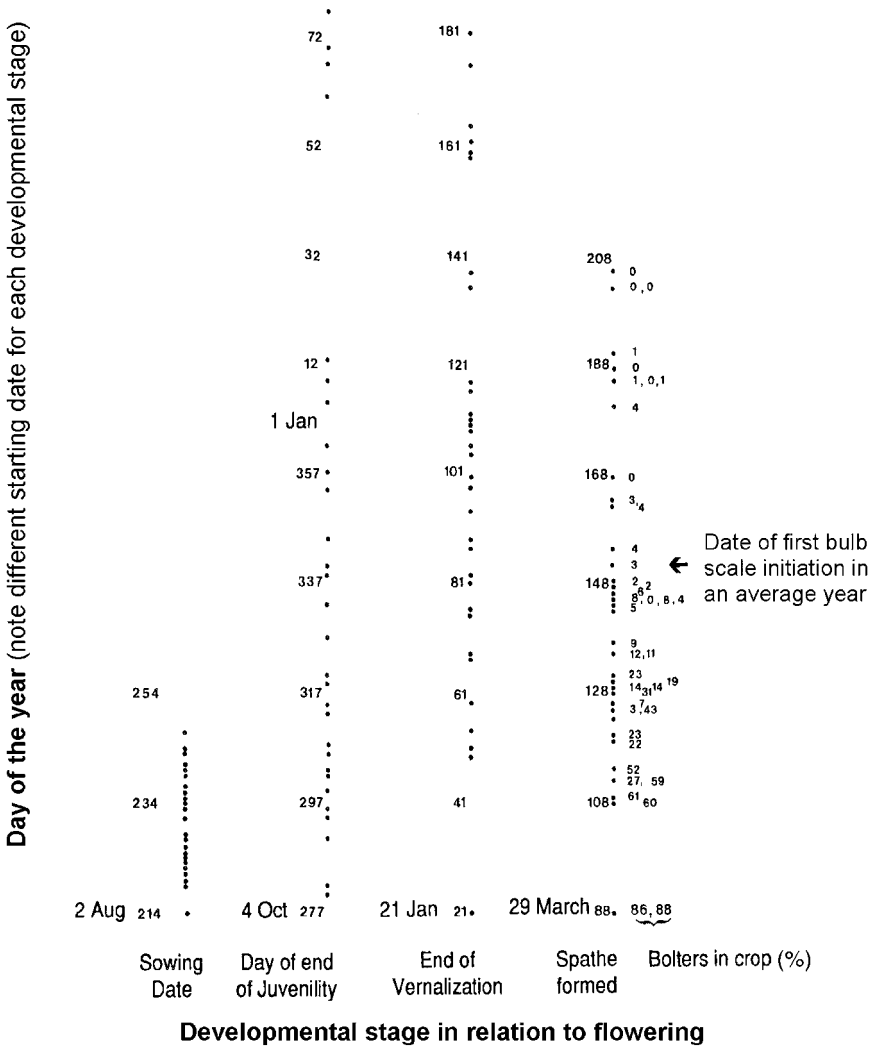

Fig. 4.43. The range of dates on which a developmental model predicted that various stages of inflorescence development would have been reached following sowings made between 2 August and 4 September during the years 1973 to 1988 at Wellesbourne, UK for cv. 'Senshyu Semi-globe Yellow' (from Brewster, 1997b).

SHALLOTS

Flowering

Shallots have traditionally been propagated vegetatively (Messiaen *et al.*, 1993), but more recently seed companies from both The Netherlands and Israel have introduced both temperate and tropically adapted cvs grown from seed (Rabinowitch and Kamenetsky, 2002). Experiments to induce flowering in traditional vegetatively propagated types have shown that some flower readily whereas others do not flower (Krontal *et al.*, 2000; Esnault *et al.*, 2005). Flowering is undesirable in the vegetatively propagated crop and, as with garlic, it has probably been selected against for many generations.

Studies on a short-day clone derived from Thailand that flowers and seeds readily in Israel have established that the requirements for flower induction are similar to those of onion (Krontal *et al.*, 2000). The optimal temperature for floral induction is 5–10°C; inflorescences can be induced in growing plants or within stored bulbs, and warm temperatures (29/21°C d/n) after an inductive cold treatment, prevent flowering. Inflorescence initials formed after the production of only six leaves, including primordia, following a mid-October sowing in Israel (Krontal *et al.*, 1998). The more bolting-susceptible cvs of onion become sensitive to vernalizing temperatures after seven leaves are initiated (see Fig. 4.36), but at least one and usually two or three further leaf primordia are initiated before the shoot apex becomes floral, thereby giving a minimum of about nine leaf initials before the floral apex. Therefore, juvenility ends at an earlier physiological age in this tropical shallot than in any bulb onion so far investigated.

From a study of two tropical and one temperate shallot cvs grown from seed, the data of Tabor *et al.* (2005) show that the tropical cvs needed, respectively, 3.50 or 4.75 visible leaves (dry weight about 0.06g) – probably equivalent to 6.50 or 7.75 leaves including primordia – to be 50% responsive to vernalizing temperatures. The temperate cv needed seven visible leaves (d.w. about 0.26g), equivalent to ten leaves with primordia. These authors emphasized that the plants had to be considerably larger than this to achieve near 100% flowering. These sizes are similar to those found for bolting-susceptible and bolting-resistant cvs of bulb onion, respectively (see Fig. 4.36).

Esnault *et al.* (2005) investigated the conditions needed to induce flowering in the traditional Jersey long and half-long shallot types, which are vegetatively propagated in France. They started with stored bulbs harvested in summer and found that 1 month of high-temperature storage with periods at 35 and 40°C during September or October improved sprouting and growth after an October planting, and increased flowering in the most bolting-susceptible type. The highest level of flowering was obtained by planting bulbs in a greenhouse at 16.5/13.5°C d/n for October and/or November so that they sprouted and grew two leaves, followed by 3 months in a phytotron at 10/6°C d/n with a 12 h photoperiod. This gave 94% flowering in the half-long cv. 'Mikor', which has a

high level of bolting when autumn-planted in the field; 34% flowering in the long-type 'Longor', which rarely flowers in the field; but no flowers in cv. 'Jermor', another long type that does not bolt naturally.

Taken together, these investigations indicate a range in the flowering responses of shallots. Some tropical types flower easily when exposed to cool temperatures, while some temperate types can be induced to flower given sufficient time under cool conditions when they are large enough. However, some strains fail to flower when exposed to long periods at temperatures normally favourable for flower initiation.

WAKEGI ONION

Growth and bulbing

The diploid hybrid between *A. fistulosum* and shallot type *A. cepa*, *A.* × *wakegi* is grown in eastern Asia, from Korea to Indonesia, for its readily branching green shoots which are harvested in the spring (Inden and Asahira, 1990). In the late spring and early summer it forms bulbs which remain dormant until late summer or autumn planting in some cvs. It is vegetatively propagated only. Fujieda *et al.* (1980) compared 202 clones from Korea, Japan and Taiwan and grouped them into two broad 'ecotypes', the 'Southern' types and the 'Japanese' types. The 'Japanese' types grew slowly in the winter but luxuriantly in the spring and formed bulbs which stored well over the summer. The 'Southern' types continued to grow through the winter and bulb earlier in the spring, but the bulbs did not become fully dormant. Within these two broad ecotypes, 22 subgroups characterized by leaf types were described.

Physiological studies on bulb formation in *A.* × *wakegi* show striking parallels in the environmental control of bulb formation with onion (see Fig. 4.33). Bulbing is promoted by long photoperiods, and 'Southern' types bulb more strongly than 'Japanese' types in a given photoperiod, and also bulbing is accentuated in dry soil conditions (Okubo *et al.*, 1981). Growing temperatures of 20°C are optimal for bulbing of both Japanese and Indonesian cvs (Okubo *et al.*, 1999). Yamazaki *et al.* (2003) investigated the effects of the temperature at which mother bulbs were stored before planting on both growth and bulbing after planting using the cv. 'Kiharabansei no.1'. Bulbs kept at 5 or 15°C for 35 days before planting were then grown at 20°C under photoperiods ranging from 11 to 14 h. Bulbs did not form under 11 or 12 h photoperiods but the cold-stored plants bulbed strongly under 13 h photoperiods, with all shoots forming bladeless bulb scales (see Fig. 4.26) after 46 days, whereas the warmer-stored plants did not bulb. In 14 h photoperiods the plants from both storage temperatures bulbed but the cool-stored ones had a higher bulbing ratio. Therefore, low-temperature bulb storage did not induce bulb formation in the shortest photoperiods but it did reduce the critical photoperiod from 14 to 13 h.

Storage of bulbs for 50 days at temperatures ranging from 1 to 25°C at 5°C intervals showed that the most rapid bulbing after planting in 13 h photoperiods at 20°C was shown by bulbs stored at 10°C (see Fig. 4.44a). When bulbs were stored at 5°C for times ranging from 0 to 84 days, before planting in 13 h photoperiods at 20°C, the longer the cool storage the stronger the subsequent bulbing (see Fig. 4.44b). If bulbs that had been cold stored at 5°C for 50 days were then exposed to warm temperatures (25, 30 or 35°C) before planting, the bulb-promotive effect of cold storage was diminished and, after 42 days of warm storage, virtually eliminated.

As with onion, the rate of bulbing of *A.* × *wakegi* is influenced by the red:far-red (R:FR) ratio of the light. When bulbs of cv. 'Kiharabansei no.1' were planted in summer under a translucent film that filtered out FR wavelengths from the

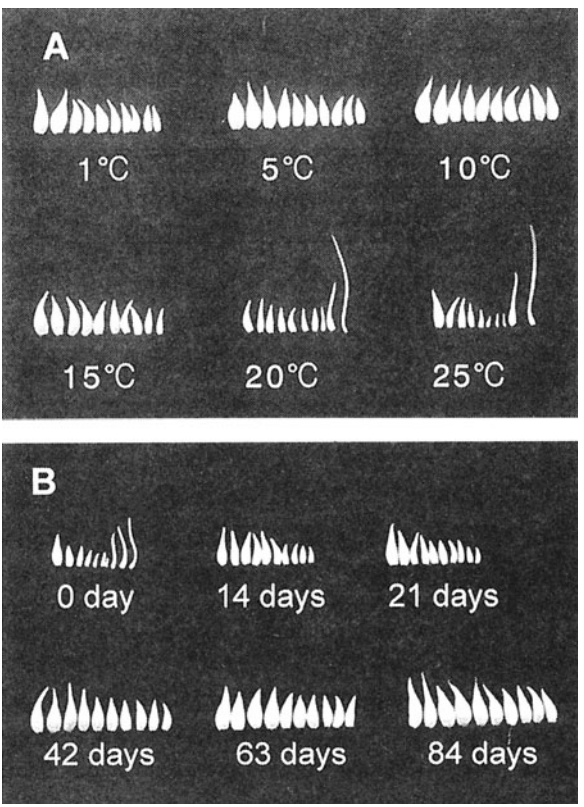

Fig. 4.44. The effect of the temperature of mother bulb storage and the duration of storage at cool temperatures on bulb development in *Allium* × *wakegi* subsequent to planting out. The greater the bulk of bladeless 'scale' leaves the stronger the bulbing. (a) Mother bulbs stored for 50 days at temperatures ranging from 1 to 25°C. (b) Mother bulbs stored at 5°C for periods ranging from 0 to 84 days (from Yamazaki *et al.,* 2003. Courtesy of *Journal of the Japanese Society for Horticultural Science*).

light to give a R:FR underneath of 2.73 as opposed to 1.22 under clear film or 1.28 in the open, the plants under the FR film did not bulb (see Fig. 4.45).

Bulbs planted in the autumn were only slightly delayed in bulbing under FR filters, whereas summer plantings were strongly inhibited from bulbing (Yamazaki, *et al.*, 1998). Subsequent experiments (Yamazaki *et al.*, 2002) showed that cool-temperature storage (5°C rather than 25°C for 70 days) of summer-planted bulbs lessened the bulb-inhibiting effect of high R:FR. This suggests that the cool temperatures following autumn planting decrease the inhibition of bulbing by high R:FR, as well as decreasing the photoperiod needed for bulb induction. Plastic film tunnels that increase R:FR can usefully extend the period of green leaf production in summer-planted *A.* × *wakegi* by preventing bulbing (Yamazaki *et al.*, 2000).

Bulb development in *A.* × *wakegi* is associated with an increase in abscisic acid (ABA) concentration in the bulb tissue and a decrease in the water potential and solute potential in the bulb scales (see Fig. 4.46). During bulb storage ABA concentration and depth of dormancy, as measured by days to bulb sprouting after planting on moist vermiculite, decrease in parallel from bulb harvest in late May until planting in early October (see Fig. 4.46).

When fluoridine, an inhibitor of ABA synthesis, was applied to plants during bulb formation, the resulting lower ABA content was correlated with faster sprouting (Yamazaki *et al.*, 1999a). Therefore the depth of dormancy correlates with ABA concentration in the bulb. However, the decrease in ABA concentration induced by fluoridine did not prevent bulbing, suggesting that ABA does not itself induce bulbing.

Cultivars differ in bulb dormancy. Cv. 'Ginoza' accumulates ABA during bulb formation but does not become dormant. On planting in moist conditions

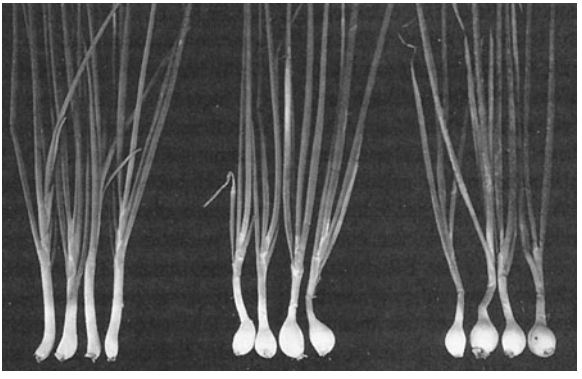

Fig. 4.45. The prevention of bulbing in *Allium* × *wakegi* by increasing the red:far-red ratio (RFR) of light. Plants grown under plastic film with much reduced transmission of far-red wavelengths (left), plants bulbing under clear plastic film (centre) and plants bulbing when grown without a film cover (right) (from Yamazaki *et al.*, 2000. Courtesy of *Journal of the Japanese Society for Horticultural Science*).

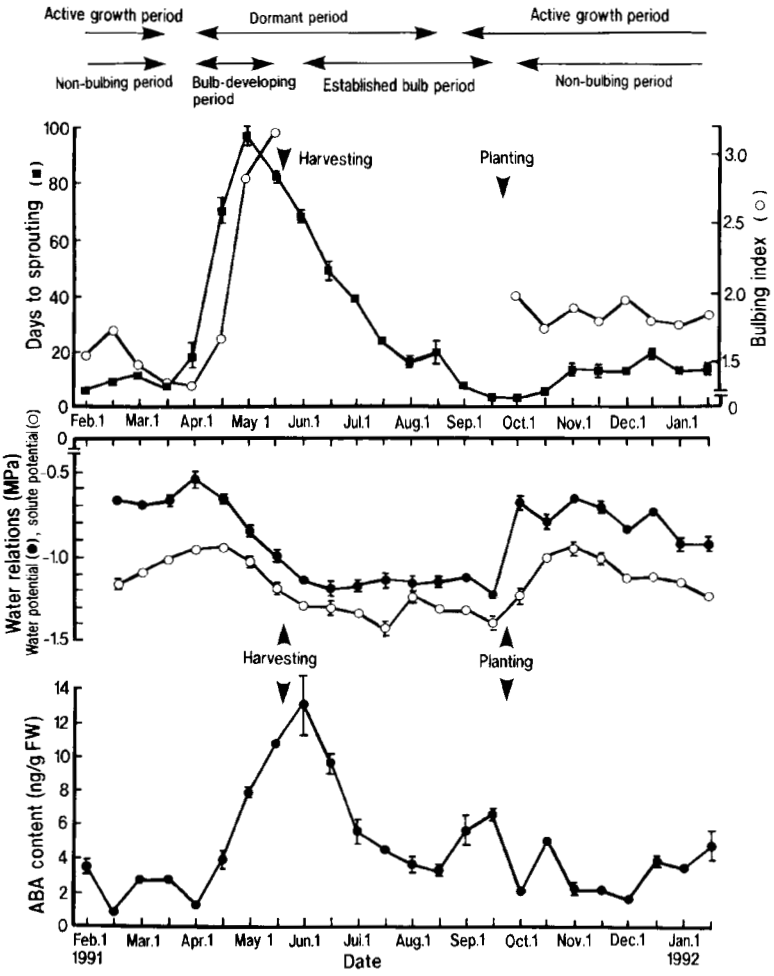

Fig. 4.46. Seasonal changes in bulb development, dormancy, water status and abscisic acid (ABA) content in the bulbs of *Allium x wakegi*. The extent of bulb dormancy was taken as the number of days to sprouting and of bulb development by the bulbing ratio (index). The bars represent standard errors based on 16, 10, 4 and 3 replicates, respectively, for the four variables listed. FW, fresh weight (from Yamazaki *et al.*, 1995. Courtesy of *Journal of the Japanese Society for Horticultural Science*).

new bulbs root rapidly and internal ABA concentrations rapidly diminish. Sprouting is also less sensitive to suppression by externally applied ABA than cv. 'Kiharabansei no.1' (Yamazaki *et al.*, 1999b). Cultivar differences in dormancy appear to parallel the extent to which ABA suppresses their bulb sprouting.

GARLIC

Growth and bulbing

The growth pattern of garlic is similar to that of onions grown from sets. Many of the physiological responses of garlic to environment are also similar to those of onion. Takagi (1990) reviewed the physiology of garlic, and papers by Mann and his colleagues (Mann, 1952; Mann and Lewis, 1956; Mann and Minges, 1958) describe extensive physiological and agronomic trials on garlic in California, the state that accounts for most of US production. This account is based primarily on these sources.

Where garlic is a major crop it is planted in the autumn or early winter and grown through to bulb harvest in the early summer. In California, planting dates range from September to March depending on location, variety and desired maturity date, but the common planting dates are October–November for cv. 'California Early' and November–January for cv. 'California Late'. Garlic is extremely hardy and can withstand considerable frost, but in areas with severe winters it must be planted in spring. In California the crop produces leaves and increases in height until May–June, reaching a maximum 10–12 visible leaves per plant and a height of 75–90 cm. Bulbing commences in late April, first with some swelling of the bases of the leaf blades and then with the swelling of the first-formed (outermost) cloves. Cloves continue to initiate in the axils of the inner foliage leaves (see Fig. 2.11) as bulbing progresses. A maximum of about 20 cloves per plant is typical of California garlic at harvest. Bulbing ratios increase from about 1.2 in vegetative plants to 5 or more when the plants mature.

Physiological studies under controlled conditions using Japanese strains that normally bolt and produce multi-cloved bulbs in the field have shown that a garlic clove may develop along several paths, depending on the sequence of environmental conditions to which it is exposed, its genotype and its size (Takagi, 1990). In certain conditions neither bulbing nor flowering may occur, and plants may make indefinite vegetative growth. Various degrees of bolting can occur, ranging from a vestigial flower stalk within the bulb to a fully developed flower stalk and umbel. In these strains, inflorescence induction seems to be a prerequisite for the formation of normal, multi-cloved bulbs.

Extremely rapid bulbing results in a single clove at the shoot apex, with no lateral buds forming before clove development and no inflorescence development. Single-cloved bulbs tend to be produced by small plants grown from small cloves or top-sets. If bulbs are stored at 2–4°C for 6 months or more, secondary bulb (clove) initiation may occur at the shoot apex actually *within* the stored bulb, an extreme that has also been observed in onion. The occurrence of all these developmental routes is subject to the influence of temperatures in storage before planting and to temperatures and photoperiods after planting.

Bulbing is stimulated by long photoperiods, warm temperatures and light of low red:far-red ratio, just as with onion. But, at least in temperate varieties,

the plants cannot respond to these factors unless they have been previously exposed to low temperatures, either as stored cloves or after planting in the field. Exposure to temperatures of 15°C or below with an optimum of 2–4°C is necessary to induce bulbing in Japanese cultivars. Cool storage of bulbs also induces flower initiation after planting, but flower induction is optimized by storage at rather colder temperatures (–2 to 2°C) than the 2–4°C optimal for bulb induction. The longer the bulbs are stored at inductive temperatures, the older the axils in which cloves may form, culminating in the potential to form an apical clove (single-clove bulb). Therefore, the developmental effect of cold storage depends not just on temperature but on its duration. For the production of normal bulbs, at least in temperate bolting varieties, the degree and duration of cold should be sufficient to induce inflorescences and break apical dominance, but should not be so prolonged as to promote bulbing at the shoot apex after planting, or to promote laterals in the outermost leaf axils, thereby favouring 'rough' bulbs.

Normally, the cold requirement will be met following an autumn planting, but if garlic is stored at 20°C or above and then planted in the late spring when mean temperatures are already warm, then the plants fail to bulb and mature and make continued leaf growth into the autumn. There is an interesting parallel with onion sets here, where warm (27–30°C) storage delays bulbing compared with cool storage, although it does not actually prevent bulbing in the case of onion. To produce measurable effects on subsequent bulbing, storage at controlled temperatures for 1 month or more is required. The effects of temperature on stored bulbs are reversible. Cloves from cv. 'California Late' stored for 3 or 4.5 months at 5°C matured by mid-August, whereas cloves stored at 20°C for 1.5 months following 3 months at the lower temperature were delayed in bulbing and failed to mature. Following such a reversal of bulb induction by high temperatures, bulbing can by re-induced by a further period of cool storage. Again, a parallel reversibility has been observed in onion sets.

In addition to influencing bulbing, the storage temperature of bulbs affects the rapidity of sprouting following planting, the vigour of growth and the shape of the plant after sprouting. In cv. 'California Late', cloves stored at warm temperatures (20°C or above) are delayed in sprouting and make slow growth with narrow leaves after sprouting. Cloves stored at 5–10°C sprout rapidly and produce plants with broad leaves and necks. Clove storage at 0°C delays sprouting but, when plants do sprout, leaf growth is vigorous and slender leaves are produced, which outgrow in height those from cloves stored at warmer temperatures. All these effects of storage temperature are more pronounced the longer the period of storage before planting. For cloves planted in the autumn, cool temperatures in the field after planting are likely to override any effects of pre-planting storage temperature, although this will vary with both season and location. In the mild winters of the Imperial Valley of southern California, just 8 weeks pre-planting storage at 0–10°C advanced bulbing and maturity even from plantings as early as mid-October (Mann and Minges, 1958).

Temperatures and day-lengths following planting also influence the development of the induced bulbs. Long photoperiods and high temperatures immediately after planting promote rapid storage leaf differentiation, so that cloves may form before axillary branching, resulting in single-cloved bulbs. This tendency will be strongest in plants from prolonged storage at bulb-inductive temperature. For the production of a normal, multi-cloved bulb in bolting cultivars, inflorescence initiation must occur before storage leaf differentiation, thereby breaking apical dominance and permitting the axillary buds to form, which can then differentiate storage leaves and form cloves. In non-bolting cultivars also, axillary branching should occur before storage leaves differentiate. This is favoured by cool temperatures and short photoperiods immediately following planting. Once axillary branching has occurred, increases in temperature and photoperiod will promote storage leaf differentiation and the growth of a normal, multi-cloved bulb.

If short photoperiods and cool temperatures persist after axillary branching, the branches may develop leaf blades and form side-shoots. The emergence of leafy side-shoots is also favoured by excessive N fertilizer and by spraying with cytokinins (e.g. 50 ppm benzyladenine). These lateral shoots widen and stiffen the necks of the plants in the field, and such plants are termed 'stiff-necks' by growers. The laterals may ultimately swell to form cloves and, as the bulbs ripen, the loss of a few outer sheaths exposes these outermost cloves on the bulb surface, so that the bulbs appear irregular and rough and are not enclosed by a neat, complete dry skin. The occurrence of such 'rough' bulbs (see Fig. 2.12) is a major quality defect in garlic that growers seek to avoid. Such an outcome is likely if lateral buds develop very soon after an autumn or winter planting, when the prevailing cool temperatures and short photoperiods will delay bulbing and promote the emergence of leafy side-shoots. This tendency to over-early axillary branching is a symptom of excessive cold induction in store before planting, due to overlong storage at low temperatures.

Figure 4.47 summarizes how environment influences the development of garlic. Different cultivars show quantitative differences in these responses to temperature and photoperiod. In all garlic-growing regions farmers select strains that produce quality bulbs under the prevailing climate, so such variation in response between strains is inevitable. Investigations on cultivars from tropical areas are needed to complement knowledge of the environmental responses of temperate-region garlic.

Because of the adaptation of garlic cultivars to local climate, controlled temperature storage of planting material is little used in practice. However, the physiological information obtained from these studies is useful when introducing garlic to new regions, and for understanding cultural problems in abnormal seasons. For example, the occurrence of 'rough' bulbs in commercial crops in California is associated with abnormally low temperatures during storage, or in the field after planting (see Fig. 2.12).

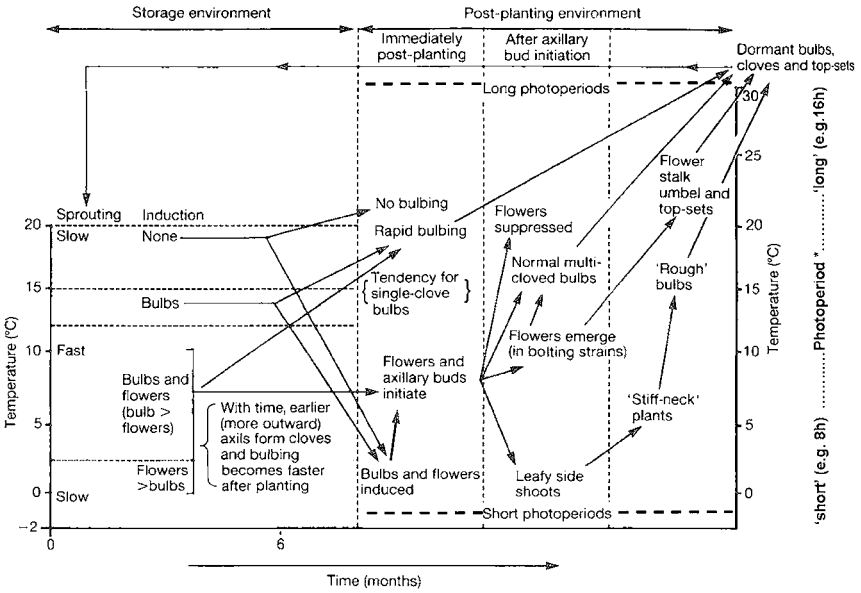

Fig. 4.47. A summary of the effects on garlic sprouting, bulbing and flowering of temperatures during storage and of temperatures and photoperiods after planting.

Flowering

The discovery of seed-fertile garlic in central Asia (Etoh and Simon, 2002) raised the possibility of improving garlic using conventional crossing rather than clonal selection and has increased interest in how to achieve normal flower development in garlic. This is not easy, since ten millennia of selection for bulbs have resulted in the suppression of florigenesis. Garlic genotypes vary considerably in their ability to produce scapes, umbels, fertile pollen and receptive stigmas (Etoh and Simon, 2002: Kamenetsky *et al.*, 2003). As discussed above, inflorescences are induced by subjecting plants or stored bulbs to low temperatures (–2 to 2°C optimum in Japanese cultivars (Takagi, 1990)). The differentiation of inflorescences did not occur within the stored bulb (see Fig. 2.18) but after planting, in the study by Kamenetsky and Rabinowitch (2001). Inflorescence differentiation following low temperature induction is favoured by growth in relatively cool temperatures and short photoperiods (e.g. below 13°C and 12 h for Japanese cvs). These conditions cause slow inflorescence initiation and emergence, but they slow bulbing more than inflorescence formation. As with onion, inflorescence development and bulbing 'compete' during this phase so that bulbing, which is favoured by long photoperiods and high temperature, tends to prevent or arrest inflorescence emergence.

Various degrees of arrested inflorescence development are commonly seen in garlic, ranging from a vestigial flower stalk within an apparently normal bulb,

through a short stalk with top-sets surrounded by the outer bulb membrane, to a short emerged stalk crowned by a cluster of top-sets. After a certain point following inflorescence emergence, rapid stalk elongation and the development of flowers and top-sets are promoted by warm temperatures and long photoperiods, again, as is the case with onion.

Kamenetsky *et al.* (2004) investigated the conditions needed to produce normal flowers in a clone from Russia (see Fig. 2.18). They distinguished four phases in reproductive development: (i) transition of the apical meristem to a reproductive state; this occurred most rapidly following cool storage of the bulbs and growth in long photoperiods; (ii) scape elongation, this was favoured by low storage and growing temperatures and long photoperiods; (iii) inflorescence differentiation; (iv) completion of floral development to anthesis. A temperature of 20/12°C (day/night) and a photoperiod of 10 h interrupted by just 1 week of 20 h photoperiods during scape elongation resulted in normal anthesis. A temperature just 3°C higher caused young flower buds to abort. Without the 1 week of long photoperiods the scape aborted and never emerged from the pseudostem. With more than 1 week of long photoperiods vegetative top-sets formed on the inflorescence, and these grew and squashed the developing flowers. So, with this clone, a very precise sequence of temperatures and photoperiods was required to achieve normal anthesis. Suppression of the whole inflorescence or suppression of florets by top-sets occurred outside all but a narrow combination of conditions.

LEEK

Growth and development

In contrast to bulb onions and garlic, leek is harvested as a growing shoot. The objective in crop production is to produce shoots of marketable size before the plants bolt. Therefore, it is useful to understand what controls flower stalk initiation and development relative to vegetative growth. The rate of elongation of flower stalks, once initiated, clearly shows some seasonality, and visible bolting is concentrated in the long photoperiods of spring and summer. However, the main variable in the 'race' to produce a marketable-sized leek before the plant visibly bolts is not the rate of flowering, but the rate of growth. In fertile soil, growth rates are primarily determined by temperatures and light levels. Premature bolting is a problem from very early plantings, which grow slowly because of low temperatures in the early spring, and from late summer and autumn plantings, where the low temperature and light levels of winter restrict growth rates, and the plants fail to achieve marketable size before bolting occurs in the spring.

Early vegetative growth can be described by fairly simple rules involving temperature, light and leaf number. For spring-sown leeks in field conditions, both the number of leaves initiated at the shoot apex, the number of leaves

emerged from the top of the pseudostem, the number of fully expanded leaves (on which the ligule at the base of the leaf lamina can be seen) and the number of senescent leaves show straight line increases when plotted against accumulated day-degrees above 0°C (see Fig. 4.48).

For cv. 'Autumn Mammoth', Fig. 4.48 shows that leaves were initiated at a constant rate of one per 92°C days (base temperature 0°C) and that leaves appeared at one per 135°C days. Leaves took longer to appear than to initiate, not because leaf initials accumulated at the shoot apex, as with cereal plants, but because the pseudostem increased in length by a constant amount for every leaf that emerged. Leaf extension growth occurs in the first 3–4 cm above the apex and the rate of extension was almost the same for successive leaves. Hence, although the rate of elongation of successive leaves was the same (per degree-day), every leaf had to grow further than its predecessor to appear. The process is summarized in simple mathematical terms by the equation:

DD per leaf appearance = DD per leaf initiation + Additional pseudostem length per leaf/Rate of leaf elongation per DD (Eqn 4.23)

Here, DD stands for day-degrees above 0°C (Hay and Kemp, 1992).

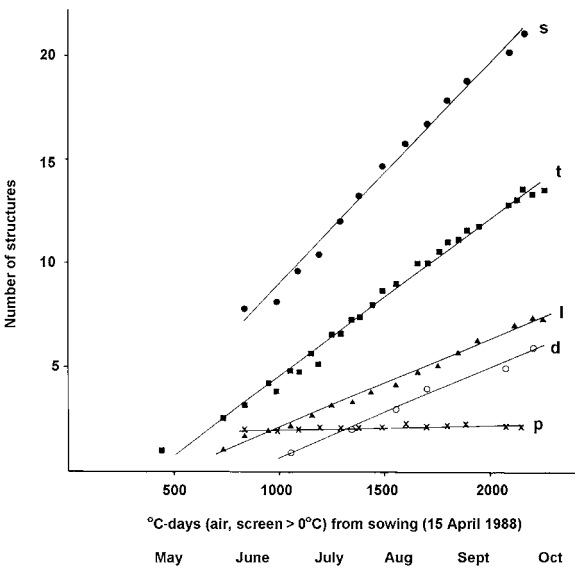

Fig. 4.48. Leaf development in leek cv. 'Autumn Mammoth' grown from a mid-April sowing in Scotland. Changes with accumulated thermal time (base 0°C) in the total number of leaf structures initiated (s), the number of leaf tips visible above the leaf sheath (t), the number of fully extended leaves with visible ligules (l), the number of leaves that were at least 50% senescent (d) and the number of primordial leaves at the shoot apex (p). The lines were fitted by linear regressions on data from 20 plants per sample date (from Hay and Kemp, 1992. Courtesy of *Annals of Applied Biology*).

The rate of ligule appearance (which indicates full expansion of a leaf blade) was slower than leaf tip appearance, showing that the duration of leaf expansion progressively increases for the first eight to ten leaves. As a consequence, in cv. 'Autumn Mammoth', each leaf was about 6 cm longer than its predecessor, and also about 0.45 cm wider (see Fig. 4.49). Cultivars differ in rate of leaf initiation, appearance and elongation per degree-day. Also, these rates tend to be higher in bright, sunny years than in dull seasons, suggesting a possible influence of light as well as temperature on these relationships. This would not be surprising, since the growth rate of leek seedlings is more sensitive to daily light income than are other crops (see below).

The growth in weight of leek seedlings has been shown to be well modelled by Eqn 4.18. The constant p in this equation is the relative growth rate per 'effective day-degree' (EDD). Effective day-degrees are day-degrees above the base temperature, T_B, modified by an effect of daily photosynthetic radiation income, R, using the constant f (Scaife *et al.*, 1987) (see Eqn 4.19b). Leek cv. 'Winterreuzen' has values of T_B = 5.9°C, p = 0.015/EDD and f = 0.146 MJ/m^2/DD. The f value is higher than for any of nine other crops studied, the base temperature for growth T_B is typical of many temperate vegetable species and p is low compared with other species (Brewster and Sutherland, 1993). The latter indicates an intrinsically low potential growth rate.

Hence leeks need a long growing season to produce plants of marketable size given their small seedling weight at emergence (about 0.002 g dry weight). The high value of f shows leek seedling growth rate to be particularly sensitive to daily light income. Probably the narrow, upright leaf habit, which is ill-

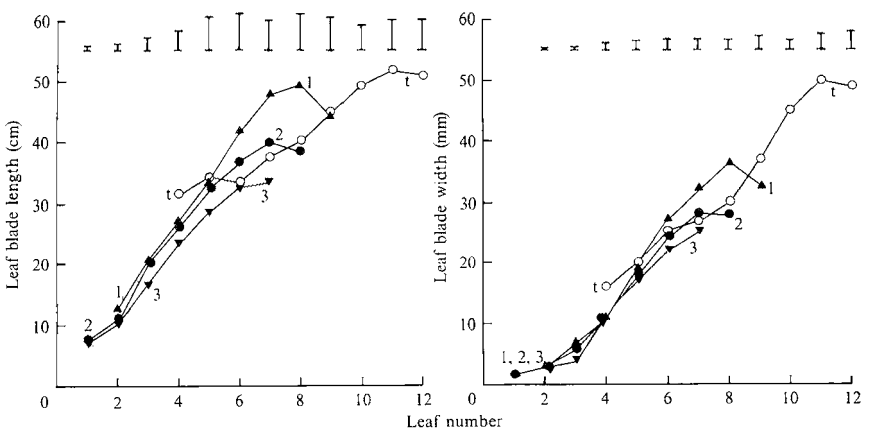

Fig. 4.49. The dimensions of fully expanded leaf blades of leek plants cv. 'Autumn Mammoth' from three spring sowings (1, 2, 3) and one transplanting (t) in the same season in Scotland. The vertical bars indicate standard errors of means x 2 (from Hay and Brown, 1988. Courtesy of *Annals of Applied Biology*).

adapted to light interception, is the cause of this. Using this relationship it is possible to predict growth rates in conditions of varying temperature and light, such as may occur in the field or in a glasshouse used for plant raising, providing growth is not restricted by lack of water or nutrients. As the plants get larger they begin to shade each other, and competition for light will cause the growth rates to diverge below the prediction of this equation. The higher the plant density the sooner this will occur.

Crop growth can continue to a ceiling or potential yield that probably varies with both temperature and daily light income and, therefore, with time of year and region. Well-watered, well-fertilized, early-planted leek crops do indeed reach a plateau of total shoot dry matter yield of around 1200g/m^2 (about 120 t/ha fresh weight) in high summer (see Fig. 4.50).

Later plantings plateau at a lower yield during autumn and winter, probably because growth rate is slowed by low temperatures, and also because the average daily light income is insufficient to sustain summer yield levels. The fact that high-yielding, summer-grown crops tend to decline in yield when left in the field over winter, due to the rotting of some leaves and the death of the smaller plants, supports the latter view. As a consequence of these effects, leek yields decrease the later in the season they are planted. The yields attained correlate with both accumulated day-degrees and accumulated solar radiation (light) during the growing period (see Table 4.8).

The diameter of the pseudostem or 'shaft' is often the important criterion of marketability of leeks, and Wurr *et al.* (1999) took a diameter of 15 mm as the minimum for marketable early leeks in the UK. From field trials they found that shaft diameter in early leeks was related to effective day-degrees (EDD)

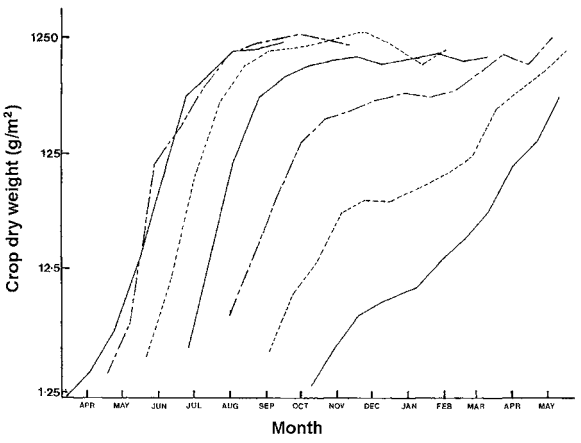

Fig. 4.50. Shoot dry weight yields of leek cv. 'Autumn Mammoth Goliath' grown at a density of 25 plants/m^2 with abundant irrigation and nutrients from a succession of plantings at Wellesbourne, central England (note log scale for crop dry weight).

Table 4.8. Aspects of leek cv. 'Splendid' as affected by planting date at Wellesbourne, UK (from Salter *et al.*, 1986).

Aspect	Planting date	
	10 April	3 July
Yield 168 days after planting (t/ha)	69	26
Day-degrees > 6°C from planting to harvest	1403	1203
Accumulated solar radiation (MJ/m^2) from planting to harvest	2938	1733

accumulated since planting, using a base temperature of 6°C and an f value (Eqn 4.19) of 0.6 (see Fig. 4.51). Accumulated EDDs with these optimal constants were a better predictor of diameter than accumulated day-degrees, time since planting or radiation accumulated since planting.

Although bulbing is uncommon in leeks, 'bulbiness' can constitute a quality defect. Strong bulbing, with the formation of bladeless inner scale leaves, has been induced under 24 h photoperiods (Dragland, 1972). As with most features of leeks, there is wide plant-to-plant variation in the extent of bulbing in these conditions. Bulbs are also frequently seen at the base of the flower stalk (van der Meer and Hanelt, 1990). Low soil temperatures also favour bulbiness, possibly because of an accumulation of unused carbohydrate at the base of the pseudostem (Dragland, 1972).

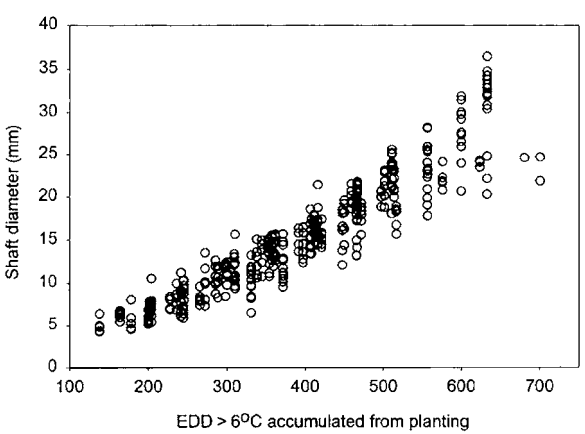

Fig. 4.51. The relationship between leek sheath diameter and the accumulated effective day-degrees from planting derived from seven experiments at Wellesbourne and in Cornwall, UK. The best-fitting Effective Day Degree (EDD) units were defined by: $EDD^{-1} = DD^{-1} + 0.6.R^{-1}$, where DD are day-degrees with a base of 6°C and R is the total solar radiation in MJ/m^2 for each day (from Wurr *et al.*, 1999. Courtesy of *Journal of Horticultural Science and Biotechnology*).

Flowering

Experiments using controlled environments indicate that flower induction in leeks occurs most rapidly between 2 and 8°C and that the percentage of plants induced increases with the duration of cold exposure up to at least 6 weeks (Wiebe, 1994; Fig. 4.52). Seedlings weighing 2 g fresh weight with four to five visible leaves were much more responsive than smaller plants, indicating a juvenile stage in young leeks when vernalizing temperatures are ineffective. Exposure to 22°C immediately following a cold treatment reduced the percentage bolting and therefore had a devernalizing effect. Exposure to a 16 rather than a 10 h photoperiod during vernalization slightly reduced the percentage bolting, but the effect was small at the near-optimal inductive temperature of 5°C.

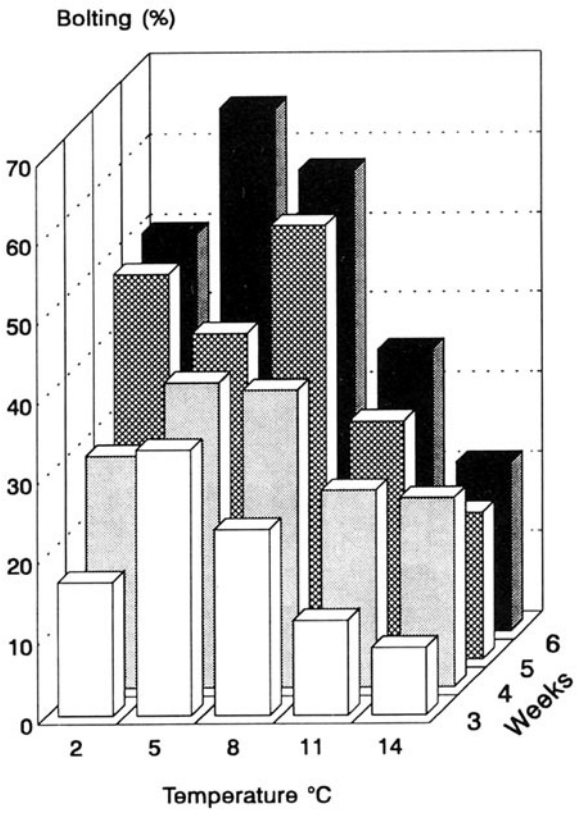

Fig. 4.52. The effects of vernalization temperature and the duration of vernalization on the percentage of plants bolting in leek cv. 'Alma'. Following the treatments shown the plants were grown at 15°C for 2 weeks and then transplanted to the field, where the numbers subsequently bolting were recorded (from Wiebe, 1994. Courtesy of *Scientia Horticulturae*).

Dragland (1972) also observed more and earlier bolting at cooler temperatures within the range 12–18°C. He also noted that flower stalks elongated faster the longer the photoperiod over the range 9–24 h, indicating that once inflorescences are initiated their rate of growth increases with photoperiod, as is the case with onion provided bulbing does not suppress the scape. Using a statistical analysis of temperatures and flowering from leeks growing from a range of planting dates at two sites, with and without protective crop covers, Wurr *et al.* (1999) concluded that 7°C was optimal for inducing flowers in cv. 'Prelina'. The strongest influence on flowering was the duration of temperature in the 4–8°C range during the 42 days subsequent to the plants reaching the three visible leaf stage, suggesting an end of juvenility at an earlier stage than four to five leaves of Wiebe (1994).

In summary, the control of flowering in leek is similar to that in onion, with a juvenile stage before which vernalizing temperatures are ineffective, an optimum temperature for vernalization around 7°C falling off to zero flowering when plants are exposed to temperatures of 18–20°C, and devernalization possible from temperatures of 22°C and above. Elongation of scapes is promoted by both long photoperiods and warmer temperatures (Wurr *et al.*, 1999).

JAPANESE BUNCHING ONION

Inden and Asahira (1990) grouped *A. fistulosum* cvs into three ecological groups. Those from regions with cold winters ('Cool Region Group') like Korea, northern China and northern Japan are dormant in winter, grow quite slowly in mean temperatures around 5°C and grow well at mean temperatures of 25°C and above. The 'Warm Region Group' from southern Japan, Taiwan and southern China do not have winter dormancy, grow well at mean temperatures around 5°C but not well at summer mean temperatures of 25°C and above. The 'Intermediate Region Group' do not have winter dormancy and grow well at both the cool and warm temperatures specified above. The optimum temperature range for growth, germination and photosynthesis is 15–20°C.

The plants are grown for either green leaves or the succulent pseudostems, which may be elongated and blanched by earthing-up. Flowering (bolting) is undesirable because the seedstalks are hard and unpalatable (Yamasaki *et al.*, 2003). Flowering is induced by exposure to cool temperatures when the plants are larger than a certain critical size. The cv. 'Kaga' (Cool Region Group) must have initiated 11 or 12 leaves corresponding to a pseudostem diameter of 5–7 mm before it can respond to flower-inducing conditions. Plants of the Warm Region Group cv. 'Pei Chang' respond to vernalizing temperatures when the pseudostem is just 4.5 mm in diameter (Inden and Asahira, 1990).

Yamasaki and colleagues (Yamasaki and Miura, 1995; Yamasaki *et al.*, 2000a,b,c, 2003) have investigated vernalization and bolting in cv. 'Asagi-

kujo' of the Warm Region Group, cv. 'Kincho' of the Intermediate Region Group and cv. 'Cho-etsu', which is later bolting than the other two and which requires longer at cool temperatures for flower induction. Comparing night temperatures of 3, 7, 11 or 15°C established that 7°C was the optimum for vernalization, with a 20°C day temperature for 8 h per day. This was indicated by the highest percentage of plants developing an inflorescence, the lowest number of leaves to the inflorescence initial, the most advanced stage of the inflorescence initials after 30 or 60 days of cool treatment and the most rapid bolting after transfer to 20°C minimum. Some flowering occurred with a night temperature as high as 15°C in the warm and intermediate region cvs 'Asagi-kujo' and 'Kincho', respectively, but this was too warm to vernalize cv. 'Cho-etsu' (Yamasaki *et al.*, 2000a). Day temperatures of 26.5 rather than 20°C with a night temperature of 7°C reduced flowering in cvs 'Asagi-kujo' and 'Kincho'. For cv. 'Cho-etsu' a day temperature of 20°C was less favourable for flowering than 13.5°C. The duration of vernalization at 20/7°C d/n needed for near 100% inflorescence induction was about 40 days for cv. 'Asagi-kujo', 50–60 days for cv. 'Kincho' and more than 75 days for cv. 'Cho-etsu'.

Short photoperiods (8 h) accelerated inflorescence induction compared with long photoperiods (16 h) in plants given a temperature regime of 16 h at 7°C and 8 h at 20°C, and long photoperiods (16 h) before cool treatment slowed induction (Yamasaki *et al.*, 2000b). As with onion, low nitrogen promotes flower initiation and leads to swelling of the leaf sheaths (Yamasaki and Tanaka, 2005). Once inflorescences had developed to the floret initiation stage, long photoperiods accelerated scape elongation. Temperatures of 35°C were devernalizing and suppressed inflorescence development. By growing plants from mid-December to mid-April in plastic tunnels in which maximum daytime temperatures of 35–40°C occurred, and by also extending the photoperiod in the tunnels to 16 h using incandescent lamps, bolting was prevented in cvs 'Asagi-kujo' and 'Kincho' (Yamasaki *et al.*, 2003). Using this technique it should be possible to extend the season of marketability of these two cvs until June in Japan.

In summary, the requirements for flowering in *A. fistulosum* are similar to those of onion in that there is a juvenile phase, the size at the termination of which increases from warm region to cool-region cultivars, an optimum temperature for vernalization of 7°C or slightly higher (Yamasaki *et al.*, 2000a) and a time requirement for induction under optimum vernalizing conditions varying from 30 days to more than 75, the time needed being longer for cvs of cool regions. Long photoperiods during vernalization slow inflorescence development, in contrast to onion where they can accelerate the process (see Fig. 4.40). Flower initiation can occur in temperatures as warm as 15°C in warm and intermediate region cvs but high temperatures, starting at about 20°C in cool region cvs and 27°C in warm and intermediate region types, are inhibitory to floral development.

RAKKYO

Bulb development in Rakkyo occurs in response to long photoperiods and is favoured by temperatures in the range 15–25°C (Toyama and Wakamiya, 1990). In Japan, inflorescences differentiate in Rakkyo in late May–June, and they elongate and bolt in the autumn, with the flowers opening in September. Rakkyo is therefore unusual among the vegetable alliums in initiating its inflorescences in the warm season. Plant size is important for flowering: plants grown from mother bulbs weighing 3 g or less do not flower and a mother bulb weight of about 11 g results in 50% flowering. Flowering is inhibited by exposing plants to short photoperiods from mid-April to mid-June, and accelerated by exposure to longer than natural photoperiods during this period (Toyama and Wakamiya, 1990).

CHIVES

Unlike the bulb-forming crops, chives are winter dormant and the onset of dormancy is triggered by the declining temperatures and shortening photoperiods of autumn. In dormant plants there is no leaf growth even under ideal growing conditions – for example, at 20°C under good lighting. The extent of growth on transfer to such standard conditions can be used to measure the degree of dormancy. Research on German cultivars has shown that the onset of dormancy is stimulated by exposure over a period of 4–6 weeks to photoperiods of less than about 14 h. The optimal mean temperature for inducing dormancy is about 14°C, and a wide day/night fluctuation around this mean is more effective than a more constant temperature (Poulsen, 1990). During the induction of dormancy, carbohydrates accumulate in the roots and at the base of the shoots. Also, growth inhibitory substances – particularly abscisic acid (ABA) – accumulate and the concentrations of growth promoters – like auxins and gibberellins – decrease.

Dormancy can be broken by prolonged exposure to low temperatures, and also by a fairly brief exposure to extremely high temperatures. In Germany, high temperatures are used to break dormancy before planting chives in glasshouses for winter leaf production. The standard technique is to immerse the plants in water, initially at a temperature of 40°C, and allow them to cool to 25°C over a 16 h period. A temperature of 40°C for 3 h is sufficient to break dormancy, but temperatures above 44°C are lethal.

Chives normally flower at the end of May in the field. They do not usually flower in the first year following a spring sowing, so probably a period of cool temperature and short photoperiods is required for flower induction, but controlled experiments on chive flowering are needed to prove this (Poulsen, 1990).

CHINESE CHIVES

Dormancy in Japanese cultivars of Chinese chive is triggered by exposure to photoperiods of 14 h or less for 30 days. Subsequent exposure to long periods at low temperature breaks the dormancy and permits regrowth as temperatures increase (Saito, 1990).

Chinese chives require long photoperiods in order to bolt. The critical photoperiods needed are longer for Japanese cultivars than for strains from southern Asia (Saito, 1990). Many cvs will not flower in the first year after sowing, indicating that a period of cool induction may be needed after the plants have reached a critical size.

CONCLUDING REMARKS

All the edible alliums grown from seed are similar in having slow germination and emergence rates and low relative growth rates in comparison with other crop species. This, along with their erect, narrow leaves, makes them vulnerable to suppression by faster-growing weeds over a long period of early growth (see Chapter 5, 'Effects of weed competition'). If they are planted as bulbs (sets or cloves) rather than seeds, the larger propagule makes for easier and faster crop establishment.

In those species that can form bulbs and inflorescences there are striking similarities in the environmental control of these two developmental pathways. Long photoperiods stimulate bulbing, the later stages of flowering when the scape is elongating and sometimes the earlier stage of inflorescence initiation. Light spectral quality as characterized by red:far-red (R:FR) ratio modifies the photoperiodic effectiveness of light in stimulating bulbing. The lower the R:FR in an inductive photoperiod the faster the bulbing, and the minimum photoperiod for bulb induction increases as R:FR increases. Direct R:FR effects on flowering have not been reported, but high plant densities, which cause low R:FR under the leaf canopy, can increase flowering (percentage of plants bolting) (Bosch-Serra and Domingo-Olivé, 1999), indicating there may be a promotive effect of low R:FR on inflorescence induction or scape elongation.

With stored bulbs, and sometimes growing plants, a period of cool temperatures (5–13°C) can accelerate subsequent bulbing. Extended periods at such temperatures are necessary for inflorescence induction (i.e. for vernalization). Periods of warm temperature (25–35°C) applied to bulbs of onion, shallot and *A.* × *wakegi* immediately after cool treatment nullify bulbing acceleration. Extended periods at such temperatures reverse inflorescence induction and have a devernalizing effect (see Fig. 4.39). Examples where flowering has diverted into bulbing are seen at many points along the route of inflorescence development (see Fig. 4.35; Kamenetsky *et al.*, 2004). First, there are the withered young inflorescences seemingly squashed by an adjacent bulb

(see Fig. 4.38), then there are examples of one or a few bulbs forming on partially elongated scapes and finally there are fully emerged inflorescences carrying numerous bulbils that have developed by suppressing the developing florets (see Fig. 2.18e, f, g and Fig. 4.41) or after deliberately removing the florets. It seems likely that generations of selection for bulbs, which constitute an easily harvested and stored source of food and an easily cultivated propagule, have favoured bulbing in garlic and shallots to the extent that flowering and seed production is eliminated in some strains, and in other cultivars flowering can be induced only by a very precise sequence of environments each specific to a particular phase of floral development (Kamenetsky *et al.*, 2004; Esnault *et al.*, 2005).

There seems to be fine balance between the path of inflorescence development and bulb development, with warmer temperatures tending to favour the latter, although this depends on the stage of inflorescence development, as after the stage of floret development warm conditions can favour rapid progress to anthesis and seed ripening. What constitutes a long photoperiod and low temperature will vary with cultivar and the climate to which it is adapted, so we can only describe trends in bulbing and flowering responses to these variables. The absolute values of photoperiod and temperature needed to progress flowering or bulbing at a particular stage of development will be specific to a particular cv. and similar for other cvs adapted to the same or similar region.

In view of these similarities in the control of flowering and bulbing and the easy switching between the two developmental paths, it is interesting to consider how this connection evolved. It seems likely that bulbing can give a plant a better chance of survival if climatic conditions deteriorate such that flowering will not result in seed production. It also allows slow-growing plants like alliums to reach a size large enough for flowering in environments with a short growing season. Is it possible that bulbing evolved as a deviant or diverted flowering response? Do the same genes control the similar responses to environment of both developmental paths?

5

Interactions with Other Organisms: Weeds, Pests, Diseases and Symbionts

INTRODUCTION

The grower of vegetable alliums does not operate in a sterile environment, and his crops may be assailed by a variety of diseases and pests which may slow growth, lower yield and cause damage and disfigurement that renders them unmarketable. Allium crops are also particularly susceptible to competition and suppression from weeds, and the reasons for this are outlined.

The main pests and disease-causing organisms and the symptoms they can cause are briefly described. The intention is to show how scientific knowledge of weed, pest and disease biology underlies rational crop protection. Attention is also paid to the interrelations between different classes of noxious organisms. For example, allium viral diseases are vectored by pest insects and mites, pest damage can predispose plants to infection by disease-causing bacteria and fungi, and weeds often act as alternative hosts for such bacteria and fungi. This chapter ends with a section on the mycorrhizal fungi of allium roots where, refreshingly, we see an example of fungi that can be of direct benefit to the plants. Symptoms of a number of the important pests and diseases are illustrated in Plates 2 to 9.

There are several publications giving excellent colour illustrations of allium pests and diseases, along with drawings and details helpful for their identification, sometimes presented as diagnostic keys. These include the book by Schwartz and Mohan (2008) and the CD-ROMs of Maude and Ellis (2001) and BCPC (2003). Excellent illustrations, along with details of biology and control methods, are freely available at numerous web sites, particularly those of many US land-grant universities, in particular Colorado State University, which includes a link to many other 'onion and garlic' web sites (http://www.colostate.edu/orgs/VegNet/vegnet/onions.html) and the University of California, which gives a comprehensive coverage of weeds, pests and diseases (http://www.ipm.ucdavis.edu/PMG/crops-agriculture.html). The research literature on pests, diseases and weeds was reviewed in Rabinowitch and Brewster (1990b), and more recent reviews of many relevant topics may be found in Rabinowitch and

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Currah (2002). These sources have been drawn on in the preparation of this chapter.

The application of new technologies to plant pathology, in particular, has resulted in rapid progress in recent years. Diagnostics are being made faster and more precise by new molecular methods that identify pathogens by their DNA or RNA sequences, and also by the development of rapid immunological tests for pathogens (Ward *et al.*, 2004). With these techniques, rapid and accurate diagnoses can be made without the need for highly trained specialists. These methods are also opening up new fields of study relevant to plant disease. For example, it is becoming possible to investigate the interactions between mixed species of microbes, including pathogens and their antagonists, on leaf surfaces or close to roots. In addition, the rapid detection and quantification of airborne pathogen spores, along with automated electronic monitoring of the microclimate in crops, can input real-time data into weather-based models for predicting pathogen infection and epidemic development. These predictions enable fungicides to be applied only when they are beneficial.

In developed economies vegetable producers are required by supermarket buyers to supply high-quality, blemish-free produce and, at the same time, there is public and political pressure to reduce pesticide usage. Needless to say, these two requirements are often in conflict and can be reconciled only by developing more sophisticated methods of crop protection based on scientific knowledge. As an example, the models for forecasting required fungicide application, mentioned above, can reduce unnecessary spraying. Such technologies are incorporated within programmes of 'Integrated Pest Management' (IPM), which aim to control weeds, pests and diseases by using pesticides in conjunction with other aspects of crop protection, including cultural methods, resistant varieties and the encouragement of beneficial organisms.

Surveys of actual pesticide use on commercial bulb onion crops in the UK indicate a modest increase in the amount of pesticides applied in recent years (total kg/ha active ingredients (AI)) but a large increase in the number of applications, particularly of herbicides and fungicides (Thomas, 2003). Between 1986 and 1999 the mean number of herbicide sprays per crop increased from around five to nine to ten, but the weight of AIs applied increased by only 19% (Grundy *et al.*, 2003). The reason for this was a continuing trend towards more 'repeat low-dose' herbicide treatments. In the same period the mean number of fungicide sprays increased from about three to five to six (Thomas, 2003). Improvements in application technology – whereby less pesticide gets wasted on non-target surfaces – and better chemicals, which are effective at lower concentration, are both tending to limit increases in amounts applied despite increases in the number of applications. In contrast, there is a growing market for 'organic' vegetables grown without using chemical pesticides. The main limitation for large-scale 'organic' production of allium vegetables is the need for many hours of hand-weeding to produce satisfactory crops (Melander and Rassmusen, 2001).

Environmental concerns have led to increased governmental regulation of pesticide use in recent years. As a result, the costs have increased of proving the safety and efficacy of pesticides and of registering them for use on specified crops. In addition, there has been a requirement for older pesticides to be tested to modern standards and re-registered if their use is to continue to be permitted. It is now uneconomic for manufacturers to register pesticides for use on anything other than the major arable crops where the areas planted generate sufficient demand to recover registration costs. In these terms the allium vegetables, in common with other vegetables, are minor crops. Various schemes have been instigated in different jurisdictions whereby growers themselves, or a combination of growers and public bodies, finance the testing and registration of pesticides for use on these 'minor crops'. In the UK, uses for minor crops are granted by 'Specific off-Label Approvals' (SOLAs), and the costs of testing and registering for these are borne out of a research and development levy on growers. By this process it is possible to provide growers with a range of appropriate pesticides that allows them to continue production of vegetable crops economically (Chapman, 2000; Knott, 2005).

WEEDS AND WEED CONTROL

Weed control is absolutely vital for vegetable allium production. Research on the topic was reviewed by Rubin (1990) and Bosch-Serra and Currah (2002). All aspects of weed control in vegetable crops were reviewed in depth by Grundy *et al.* (2003), and this account owes much to their work.

Effects of weed competition

Vegetable allium crops are easily outcompeted by weeds, especially when directly seeded rather than grown from transplants or sets. The slow germination, low relative growth rate (RGR) and low, upright leaf canopy of alliums that never approaches total light interception, are innate features of these crops that make them weak competitors for light (see Table 4.5 and Fig. 4.1). The shallow, relatively sparsely branched root system is also ill-adapted to compete for water and nutrients against weeds (see Figs. 2.15 and 2.16). As an example, the poor competitive ability of leeks for light compared with celery, which has a higher seedling RGR and more horizontal foliage – and the consequences of these features for the suppression of groundsel (*Senecio vulgaris*) in these crops – is illustrated in Fig. 5.1 and Table 5.1 (Baumann *et al.*, 2001). Ample water and nutrients, the elimination of all weeds but groundsel and the prevention of pests and diseases ensured that the effects shown in Fig. 5.1 and Table 5.1 resulted solely from light competition between the crops and this weed.

Table 5.1. The effect of light competition from leeks or celery on the biomass of stands of the weed groundsel, *Senecio vulgaris*, which emerged at a range of dates (0, 10, 20, 30 and 40 days) after transplanting the crops. These weights were recorded 90 days after crop planting and are the means of three observations (SEM 13) (from Baumann *et al.*, 2001, Table 3).

Groundsel emergence day	Biomass of groundsel (g/m^2)				
	0	10	20	30	40
Under leek	191	137	43	39	12
Under celery	165	62	7	0.6	0.01
Groundsel only	222	–	–	–	–

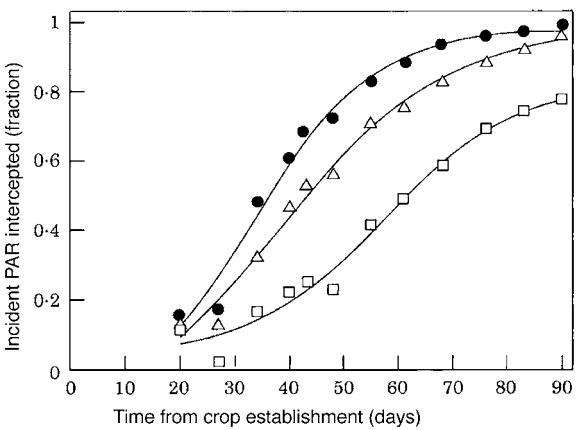


Fig. 5.1. Fraction of light (PAR) interception by stands of leek □, celery ● and a leek–celery intercrop △, growing from late May through to August in Switzerland. Plant populations were 18 and 9 plants/m^2 for leek and celery, respectively, and the intercrop was alternating rows of the two species at the same within-row spacing as in their monocrops (from Baumann *et al.*, 2001. Courtesy of *Annals of Botany*).

Experiments in the UK showed that the yield of spring-sown bulb onions exposed to competition from a natural arable weed flora on unweeded plots was only 3% of that on weed-free plots (Roberts, 1973). In these experiments the maximum relative growth rate recorded for onions was 0.12/day, whereas the weeds had a maximum of 0.18/day, and this occurred at an earlier and cooler stage of the growing season. The result of this, and the slower seedling emergence of the onions than some weeds, was that by early June the dry weight of weeds was 20-fold the crop dry weight.

The consequence of weed competition is, of course, low yield. Complete crop failure will occur if weed competition is not prevented in direct-sown

alliums. In addition, weeds cause severe problems at harvest for leafy crops like salad onions and leeks, and interfere with the drying and storage of bulb onions. Competition from weeds will reduce the mean diameter of onion and garlic bulbs, putting an increased portion of the crop into low-value, small-size grades. Weed competition will actually accelerate onion bulb initiation if photoperiods are approaching those required for bulbing (Shadbolt and Holm, 1956). Therefore, bulbs develop on younger and smaller plants than would otherwise be so, further reducing the size of the leaf canopy that supports bulb growth compared with that of a weed-free crop.

The acceleration of bulbing that can be caused by weed competition is probably due to decreases in the red:far-red ratio (R:FR) incident on leaves when shaded by weeds (see Fig. 4.33). The likely variation of weed competition from spot to spot within a field will contribute to increased variation in bulb or plant size at harvest. The presence of weeds within the leaf canopy of allium crops will restrict air flow through them, which is likely to increase relative humidity and prolong periods of leaf wetness, thereby increasing susceptibility to fungal leaf disease (see Table 5.5). For all these reasons, particularly those pertaining to quality and weed contamination at harvest, which will not be tolerated by the supermarket retailers that now sell the majority of vegetables in developed economies, there is generally a policy of 'zero tolerance' of weeds in allium vegetable crops (Grundy *et al.*, 2003).

Researchers have investigated how long weeds can be left in allium crops without causing irretrievable losses in yield and, secondly, having controlled the weeds once, how long crops must be kept weed-free so that any subsequently emerging weeds do not lower yields. In experiments on bulb onions in the UK, weeds left until 4 weeks after crop emergence did not reduce yield but, if left longer than 6 weeks, bulb yield was reduced by 4% for every day their removal was delayed (Hewson and Roberts, 1973).

Such studies have led to the specification of a 'critical period' during which the crop must be kept weed-free to ensure there will not be a serious loss of yield caused by weed competition. Following a review of research on critical periods in vegetables crops, Grundy *et al.* (2003) concluded that the critical period after emergence or planting was 4–8 weeks in spring-drilled bulb onions, 5–7 weeks in spring-transplanted bulb onions and from 4 weeks onward in spring-drilled salad onions. These critical periods concern effects on yield but not weed impacts on harvesting or quality. If there is a high density of highly competitive weeds and temperatures are conducive to rapid growth, the critical period for drilled bulb onions may commence as soon as 2 weeks after emergence. Therefore, the timing and duration of the critical period can vary with weed density, weed competitiveness and weather conditions, in particular temperature.

Dunan *et al.* (1996) took these factors into account in regression equations for the effect of duration of time before starting weeding on yields from commercial drilled bulb onion crops in irrigated fields in Colorado, USA.

Yields were expressed as relative to the maximum in each trial (weed-free plot yield), duration of competition (DC) was expressed in units of thermal time (TTUs) from sowing (see Chapter 4), thereby including effects of temperature as well as time, and weed competition was quantified as the 'weed load' (WL = the sum over all the species present of their plant densities multiplied by 'their competitiveness indexes'). Different weed species were given a 'competitiveness index' based on the degree to which their presence had been found to lower maize yields. Up to 75% of the variation in relative yields between fields and seasons caused by weed competition was explained by regressions on DC and WL. For a weed flora of average competitiveness it took 220 TTUs (base temperature 7.2°C) before commencing weeding to cause a 5% decrease in relative yield with 20 weeds/m^2, and 315 TTUs with five weeds/m^2. Relative yields decreased at about these respective rates for each weed density as the thermal time before weeding was prolonged. Equation 5.1, which describes the response surface shown in Fig. 5.2 (Dunan *et al.*, 1996, Fig. 2) was the most meaningful summary of the results:

$$\text{Onion Relative Yield} = 0.83 - \{1.5.10^{-5} \times DC^{1.198} \times [WL/(1 + 0.2 \times WL)]\} \quad \text{(Eqn 5.1)}$$

Several dynamic simulation models of weed competition in allium crops have been developed (Dunan *et al.*, 1999; Baumann *et al.*, 2002; Grundy *et al.*, 2005). These all model competition for light and therefore apply to the situation in crops without significant competition for water or nutrients, a reasonable assumption for irrigated crops. In these models, onions and weeds are assumed to grow as they would in the absence of competition until the leaf canopy approaches closure (i.e. when Leaf Area Index (LAI) exceeds unity). Then, the fraction of the incident light that is apportioned to crop or weed species, and which therefore drives the subsequent growth of each species, is specified by rules considered adequate to describe the real situation. For example, in Dunan *et al.* (1999), growth rate in a competitive situation is the growth rate of an isolated plant at the prevailing temperature multiplied by a competition factor, cf_i, appropriate to the species. The competition factor models the fraction of the total incident light that the species captures. This is determined by the leaf area index of the species (LAI_i) weighted by its light extinction coefficient, k_i, derived from its equivalent of Eqn 4.1, relative to the sum of such weighted LAIs for all the species in the competitive situation. Thus, for the ith species competing among a total of n species:

$$cf_i = k_i \times LAI_i/(\sum_{i=1}^{i=n} k_i \times LAI_i) \quad \text{(Eqn 5.2)}$$

With these models it is possible to incorporate parameters that describe the growth rate of individual plants of a species (e.g. k_i and the parameters that

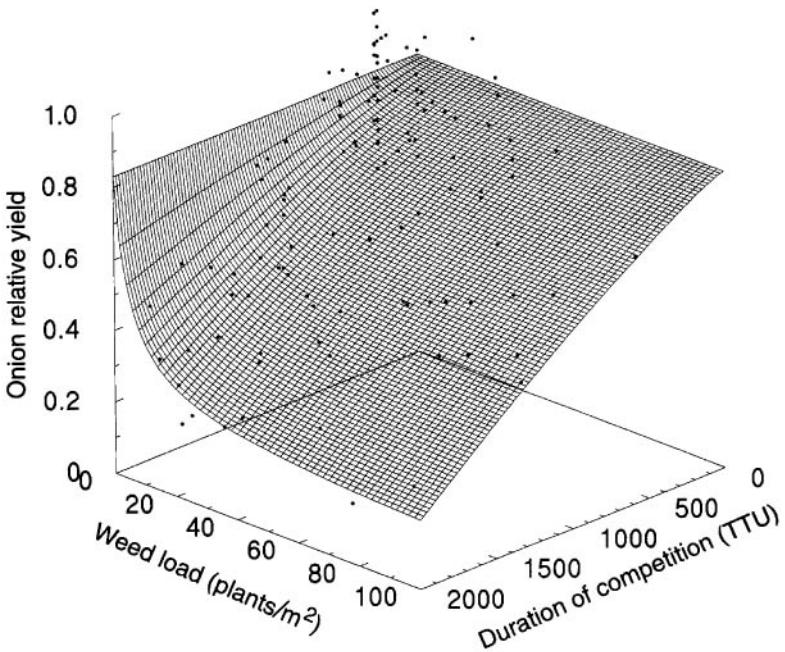


Fig. 5.2. The effect of the intensity and duration of weed competition on yields of irrigated bulb-onions in Colorado, USA. The duration of competition is expressed as thermal time units (TTU) above a base temperature of 7.2°C from sowing, and weed loads were calculated from the population densities of the weeds present weighted by a competitiveness index for each species (see text). Yields were expressed relative to the maximum (weed-free) yield in each field (from Dunan *et al.*, 1996. Courtesy of *Weed Research*).

describe relative growth rate and its response to temperature, and the partitioning of photosynthate into leaf area) into a prediction of how a competitive mixture of species will behave. These models can be used to simulate the effects of weeds or weed removal treatments on yields (see Fig. 5.3).

Models can be combined with economic information on the value of yield likely to be lost to competition from the weed species emerging in a crop and the cost of herbicide or hand-weeding treatments, thereby providing growers with a decision aid for weed control (Dunan *et al.*, 1999). By using such a decision aid, growers can maximize their economic returns from weed control treatments and apply herbicides only when there is economic benefit, thus avoiding unnecessary environmental pollution.

Providing models are shown adequately to simulate reality, they can then be used to predict outcomes form a wide range of competitive scenarios much more economically than could be done by field experimentation. The predictions from

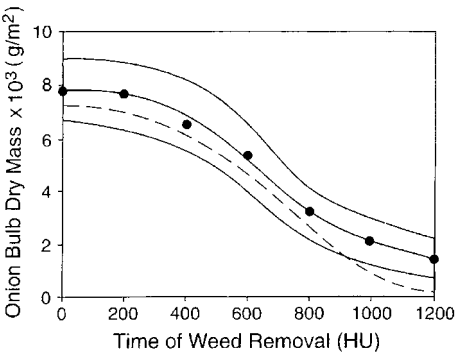


Fig. 5.3. The effects of the time for which weed competition is allowed to persist on the yield of irrigated bulb onions in Colorado, USA. The points and solid lines show observed yields and 95% confidence bands, respectively, and the broken line shows the predictions from the simulation model outlined in the text. The time of weed removal is expressed as thermal time (HU – heat units = °C-days from sowing with 7.2°C base temperature) (from Dunan *et al.*, 1999. Courtesy of the *Journal of the American Society for Horticultural Science*).

these mechanistic competition models can be quite complex and may themselves need further simple descriptive models of the responses found to summarize their predictions (Baumann *et al.*, 2002). The latter authors used their parameters for growth and light interception of leeks, celery and groundsel, grown separately, to model the consequences of growing leeks and celery as an intercrop on the yields of each crop species and on seed production by the weed. Thereby they were able to specify the optimum densities at which to interplant leeks with celery so that the stronger competitive ability of the latter could supplement the rather weak competitiveness of leeks and ensure good suppression of the weed while maintaining leek quality (i.e. ensuring leeks were of marketable size) and maximizing financial return per unit area of field. Weed suppression was expressed both in terms of the reduction in biomass of the weed and also the consequent reduction in the number of seeds shed by the weed. The fewer seeds a weed sheds the less seed it leaves in the soil weed seed-bank to infest future crops, a consideration of particular importance when managing weeds over the whole rotational cycle of crops, particularly in organic production (see below). These complex interactions are summarized graphically in Fig. 5.4.

Weed control

Herbicidal weed control

The availability of herbicides for allium vegetable crops starting in the 1940s and, becoming fully established from the 1960s onwards, enabled their production, in

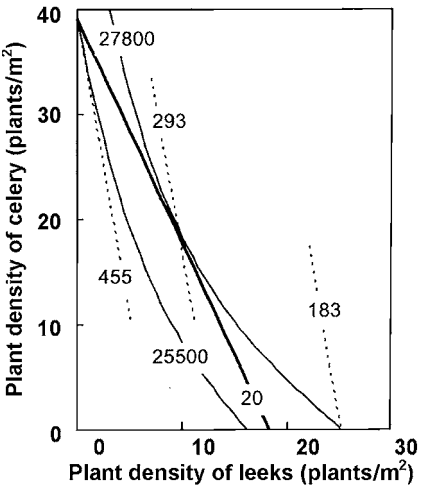


Fig. 5.4. Predictions from a simulation model for yields and groundsel seed production in transplanted leek/celery intercrops after 3 months of growth in Swiss summer weather conditions; the effects of varying the plant densities of leek and celery on total financial yield (fine lines, €/ha), on seed production (dotted lines, seeds/m^2) by 50 plants/m^2 of groundsel weeds emerging 40 days after crop transplanting, and the isoline (thick line) for minimum pseudostem diameter (20 mm) needed for leeks to be marketable. The lines are isolines showing the range of leek/celery planting densities which give the indicated financial yields or numbers of groundsel seeds. A density of 20/m^2 of leek and 10/m^2 of celery plants is near optimal, giving maximum financial yield, marketable-sized leeks and strong suppression of groundsel seed production (from Fig. 6.D of Baumann *et al.*, 2002. Courtesy of *Agronomy Journal*).

common with other vegetables, to progress from market garden to field scale. Wide rows were no longer needed to facilitate hoeing, and this allowed crop-spacing requirements to be reappraised so as to arrange plants more uniformly and thereby fully exploit the available light and soil resources, resulting in 10–30% yield increases (see Chapter 6). Bulb onion and leek crops are now commonly grown in arable rotations with crops like cereals.

The herbicidal programme for bulb onions typically contains the following sequence:

1. Non-selective pre-emergence herbicides. These are used to destroy weeds that develop before crop emergence. They may be contact herbicides like paraquat or translocated herbicides like glyphosate.
2. Pre-emergence residual herbicides. These are applied to weed-free soil and persist as a surface layer, killing weeds as they emerge. A moist soil, or rain

within 1 week of application, is necessary for these to be effective. The duration of their residual action depends on the temperature and moisture content of the soil. For example, propachlor can persist for 6–9 weeks, but breaks down more rapidly in warm, irrigated conditions. If crop emergence is slow, as with spring sowing in cool regions, the application of pre-emergence residual herbicides is best delayed until a few days before crop emergence, so that the herbicidal effect persists for as long as possible after emergence. Soil type affects the choice and dosage of residual herbicide: sandy and silt soils low in organic matter are less retentive of herbicides than soils higher in organic matter. Chlorpropham should not be used on light, sandy soils since heavy rain can leach herbicide to the roots, causing severe crop damage; and the dose rate of pendimethalin should be increased in moving from sandy to fine soil to maintain effectiveness. The herbicidal surface layer of residual chemicals is destroyed if the soil is cultivated, so such treatments must be repeated following hoeing or other soil disturbance. All pre-emergence treatments for sown crops are also suitable for use prior to emergence of sets and bulbs.

3. Post-emergence or post-planting residual herbicides. The residual herbicides propachlor, pendimethalin and chloridazon are applied post-emergence in the UK, commonly in conjunction with a low dosage of a contact herbicide like ioxynil (Grundy *et al.*, 2003).

4. Post-emergence or post-planting contact herbicides. Nowadays, applications of post-emergence contact herbicides in onions begin as early as the loop stage of seedlings (see Fig. 2.1) in the UK (Grundy *et al.*, 2003). In the early 1970s, application of this type of herbicide was delayed until after the first two true leaves had formed (Fig. 2.1) because of herbicide damage to seedlings younger than this. However, by lowering herbicide dose rate, onion seedling damage can be prevented and, by repeated spraying, weed seedlings can be destroyed while they are small and still susceptible to low herbicide doses. As a result of the adoption of repeat, low-dose programmes the average number of herbicide applications per onion crop in the UK increased from three to four in 1977 to nine to ten in 1999, but the increase in the total weight of herbicidal substances applied was only about 19%. Ioxynil is the herbicide most widely used in these repeat, low-dose applications. Onion resistance to herbicide damage increases with plant size, and therefore crops grown from sets or transplants are less susceptible than small seedlings. Herbicide resistance by onions depends on the extent and integrity of the leaf-surface wax layer (Verity *et al.*, 1981). Conditions or treatments that damage or reduce this wax layer – e.g. abrasion by blown sand, pest or disease damage, high humidity during leaf development or strong surfactants in sprays – can increase crop susceptibility to herbicide damage. The increase in herbicide tolerance with stage of growth can be dramatic. For example, the dose of methazole (now no longer available) needed to decrease onion seedling dry weight by 50% on day 14 after spraying increased 80-fold between the loop stage and the three-leaf stage (see Fig. 2.1; Verity *et al.*, 1981). The retention per unit leaf dry weight of the dye tartrazine,

following spraying, decreased 5–10-fold between the loop and the three-leaf stage. The contact angle between water and the leaf surface increased from 58° for the cotyledon, typical of a readily wettable surface, to 125° for leaf three, typical of a highly water-repellent surface. Scanning electron micrographs of onion leaf surfaces show the cotyledon to have a smooth surface covered by flat wax plates, true leaf 1 to be covered in distinct wax crystals and leaf 2 to have a micro-rough surface of crystalline wax that gives the leaf a visible 'bloom' (see Fig. 5.5). These changes in surface wax cause the decrease, with plant age, in surface wettability, the concentration of substances retained after spraying and, hence, the increase in herbicide tolerance. Where post-emergence herbicides cannot be applied until the crop has reached a tolerant stage, the crop needs to be uniformly at the same stage of growth. A prerequisite for this is a narrow spread of emergence in time, hence the need for good seedbeds and seedling establishment conditions if herbicides are to be used effectively (see Chapter 6).

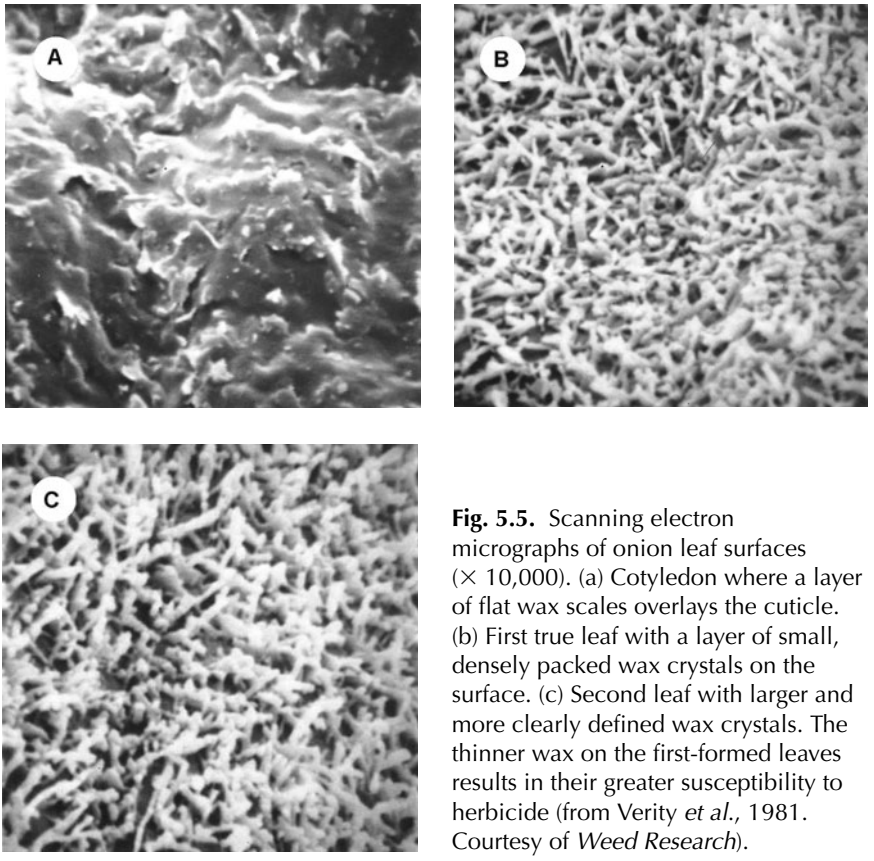


Fig. 5.5. Scanning electron micrographs of onion leaf surfaces (× 10,000). (a) Cotyledon where a layer of flat wax scales overlays the cuticle. (b) First true leaf with a layer of small, densely packed wax crystals on the surface. (c) Second leaf with larger and more clearly defined wax crystals. The thinner wax on the first-formed leaves results in their greater susceptibility to herbicide (from Verity *et al.*, 1981. Courtesy of *Weed Research*).

The choice of appropriate herbicides and application rates depends on the following factors:

1. Weed species present. Tables indicating which weeds are destroyed by which herbicide, and what dose rates are required can be found in advisory literature on herbicides and allium production, much of which is available online (e.g. Beck *et al.*, 2004; University of California, 2007); the principles involved are also discussed in Grundy *et al.* (2003). Both residual and post-emergence contact herbicides are frequently applied in combinations in order to control the whole spectrum of weeds present. Ioxynil is applied along with cyanazine to control Polygonums; fluroxypyr to control volunteer potatoes and cleavers; bentazone to control mayweeds and clopyralid to control thistles and other Compositae (Grundy *et al.*, 2003). Grass weeds – including volunteer cereals and rows of barley deliberately planted to provide shelter and protection from wind erosion damage to onion seedlings – are controlled by the graminicides fluazifop-P-butyl or propaquizafop.
2. Soil type. The type and dose of residual herbicides appropriate vary with the texture and organic matter content of soil (see 'Pre-emergence residual herbicides', above). Concern about the contamination of groundwater with herbicide residues has been a major driver of increased restriction and regulation of their use. To avoid leaching the more soluble herbicides into the groundwater, their dose rates may need lowering on light, sandy soils.
3. Crop growth stage. This determines the extent of herbicide tolerance (see above) and, therefore, the extent of selectivity between crop and weeds.
4. Weather conditions. Weather can affect herbicide tolerance and persistence. For example, the tolerance of onion to ioxynil is less in conditions of bright sun and high humidity. Residual herbicides degrade faster as soil temperature and moisture content increase, provided aeration is adequate.
5. Herbicides permitted by the regulatory authorities. The herbicide types approved for use on allium crops vary between countries (e.g. see references under point 1 above), although the countries of the European Community (EC) are harmonizing their herbicide regulation and approval systems. It is now very expensive to test a herbicide for use on a crop so as to fulfil the stringent regulatory demands of developed countries. Such testing is uneconomic for agrochemical producers for all except major arable crops. The value of the herbicide market for crops grown on a smaller area, like most vegetable crops, is too small for manufacturers to recover their costs of regulatory testing. This is causing problems for allium producers because few new herbicides are being tested and approved. Moreover, in Europe and the USA, concerns about the environmental damage from certain herbicides, notably groundwater pollution, have led to a tougher regulation of their use. Some of the older compounds have been required to fulfil newer, more rigorous criteria than applied when they were originally brought on to market, and approval for their use has been withdrawn, because either they cannot meet the new criteria or manufacturers

do not think potential sales justify the costs of testing to meet the modern regulations. Consequently, there is something of a crisis for vegetable growers, including allium producers, in that they must rely on a diminishing range of herbicides. A number of useful products have ceased to be available to UK onion growers, including alloxidim-sodium, sethoxydim, aziprotryne, chlorbufam, cyanizine, methazole, prometryn and sodium monochloroacetate (Grundy *et al.*, 2003). In the extreme scenario this could make it impossible to grow some crops economically. A more insidious danger is that reliance on a smaller range of herbicides is likely to increase the risk of weeds evolving tolerance to compounds that are applied repeatedly without alternation with herbicides having a different mode of action. In order to overcome these difficulties, trials are ongoing to find newer herbicides that are effective in vegetable alliums and to provide data to gain approval for their use. In the UK, this work is carried out by a development organization funded by growers (Knott, 2005). Given the critical need for good weed control in bulb onion crops and the need for multiple, low-dose treatments, with risk of crop damage and each needing favourable weather conditions for spraying, if onions genetically modified to be resistant to glyphosate or glufosinate were available and acceptable (see Chapter 3), weed control would probably be simplified and improved.

Herbicide recommendations for garlic are similar to those for bulb onions (University of California, 2007) – as are those for salad onions, but particular care must be taken to avoid herbicide damage to leaves, which can make the crop unsaleable (Grundy *et al.*, 2003). Leeks also need a similar herbicide programme to that for onions, often including split-dose applications starting from the one- to three-leaf stage. Since leek leaves funnel liquids towards the junction of blade and sheath, there is less run-off than with onions and they are more sensitive to post-emergence herbicides. They also collect more pesticide residue than onions, and this restricts use of some chemicals (Grundy *et al.*, 2003). Minimum intervals between the final herbicide spray and harvest are specified by regulatory authorities to avoid significant residues on the produce, and some supermarkets impose additional restrictions on herbicide use by their suppliers.

Cultural and mechanical weed control

In recent years public concerns about pesticide usage have given impetus to research on the improvement of non-herbicidal methods of weed control. Governments have banned some herbicides formerly used, particularly those found to be contaminating water supplies and, at the same time, have funded research on 'integrated' crop weed control methods to try to reduce the need for herbicides.

In many countries there is an expanding market for 'organic' produce that must be grown without the use of herbicides, and research on non-chemical weed control is relevant here. Producing alliums without herbicides is particularly difficult given their weak competitive ability against weeds. Time

requirements for hand-weeding varying from 100 to 600 h/ha have been recorded for weed control in drilled onion and leek crops, depending on the weed density present (Melander *et al.*, 2005). The requirement for 150–200 h/ha for mechanical and hand-weeding for organic bulb onions in the UK accounts for 15–30% of variable production costs (DEFRA, 2002), whereas pesticide applications as a whole represent about 15% of the variable costs of conventional, drilled bulb onions (Nix, 2006).

Because of the high cost of labour for hand-weeding, even if it is available, it is only economically feasible to grow drilled onion or leeks organically where weed numbers are low. A seedbed prepared several weeks before sowing allows the surface flush of weeds brought to the surface by prior cultivations to emerge so that they can be destroyed by flame-weeding or harrowing the top 1–2 cm before sowing the crop – this is termed a 'stale seedbed'. Stale seedbeds require crop drilling to be delayed, making them problematical when early spring sowing is necessary for bulb onion production. After emergence, weeds between the crop rows can be destroyed by steerage hoes, flaming or brush-weeders, but intra-row weeds require hand-weeding. In experiments in Denmark, a combination of stale seedbeds and inter-row weeding lowered the time requirement for hand-weeding of drilled leeks to about 50 h compared with 350–400 h for untreated plots (Melander and Rasmussen, 2001). The time needed for hand-weeding was linearly related to the number of intra-row weeds (see Fig. 5.6).

Intra-row weeds in leeks can be partially controlled by smothering, using machines that brush or ridge soil into the crop row; this also aids in blanching the leek pseudostems. Weed control is easier in bulb onions grown from multi-seeded modules (see Chapter 6), since these can be planted at a spacing that allows long-handled hoeing within the row. Weed control is generally simpler in crops grown from sets or transplants than in drilled crops because large, more robust plants are more quickly established that can withstand some damage from weed control machinery, and their shorter growth period leaves less time for weeds to get established. In temperate regions weed emergence normally peaks in the spring, after which fewer weeds appear. If the weeds from the spring flush of emergence are destroyed, those germinating later have less effect on onion bulb yield. This is another advantage of transplants as, since they can be planted later than a direct-sown crop, the spring flush of weeds can be destroyed before transplanting. Leeks also are commonly grown from spring and summer transplants, and therefore miss the worst time of year for weed emergence.

In order to achieve conditions of low weed pressure for vegetable allium production it is important to integrate appropriate weed management into the wider context of the cropping system (Melander *et al.*, 2005). Diversified crop sequences, where winter and summer crops alternate and where both spring- and autumn-sown crops are grown, can prevent the build-up of a competitive weed community adapted to a particular rotation or mode of cropping. One promising cropping system is to alternate spring-sown barley with a vegetable row crop (Melander *et al.*, 2005). The highly competitive barley crop is grown

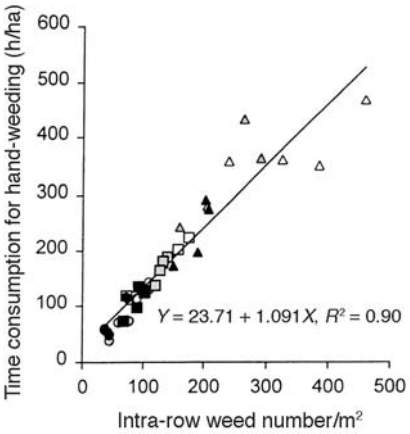


Fig. 5.6. The relationship between the number of within-row weeds and the time (hours) needed for hand-weeding of direct-sown leek crops in Danish trials. The different symbols show the effects of various non-chemical weed control treatments on the number of within-row weeds: open triangles, untreated; open circles, flaming then untreated; open squares, pre-emergence harrowing then untreated; shaded triangles, no pre-emergence treatment then hoeing; shaded circles, flaming then hoeing; shaded squares, pre-emergence harrowing then hoeing; solid triangles, no pre-emergence treatment then brushing; solid circles, flaming then brushing; solid squares, pre-emergence harrowing then brushing (from Melander and Rasmussen, 2001. Courtesy of *Weed Research*).

so as to deplete the seed-bank available for producing intra-row weeds in the following year. Wide rows in the barley crop are repeatedly inter-row hoed to turn up weed seeds and stimulate their emergence. In the next year direct sowing of the vegetable crop into these hoed bands resulted in an 80–90% reduction in intra-row weed emergence compared with a conventional system, thereby making weeding much easier (Melander *et al.*, 2005).

Costs of weeding can be lowered by ignoring weeds emerging after the 'critical period' (see 'Effects of weed competition', above), since these will have little consequence for yields. However, if such weeds are allowed to seed, the weed seed-bank in the soil is augmented and this is likely to result in higher weed populations in future years. For several weeds the number of seeds produced has been shown to increase with shoot biomass, either linearly (Baumann *et al.*, 2001) or with log seed number linearly related to log shoot biomass (Grundy *et al.*, 2004). In organic and reduced-input cropping systems that include allium vegetables, their potential legacy of increased future weediness needs to be considered. The intercropping of leeks with celery discussed above was envisaged as a cropping system that could suppress late-emerging weeds and prevent their seeds from entering the soil seed-bank (see Figs 5.1, 5.4 and Table 5.1).

Emerging technologies that may in future improve non-herbicidal weed management include the application of machine vision to the guidance of inter-row steerage hoes (Melander *et al.*, 2005) or to robotic weeding machines, for which progress has been made in distinguishing leeks from weeds (Grundy *et al.*, 2005). It has been found that drilled onion leaves need to have a height of 10 cm or more before they can withstand current methods of mechanical intra-row weeding without excessive crop damage (Melander *et al.*, 2005). In this context, it should be possible to give drilled alliums a size advantage over weeds by accelerating their emergence and early growth through the use of seed priming and starter fertilizers (see Chapter 6).

Another intriguing idea is to restrict soil cultivation to night-time so that exposure to daylight during cultivation does not break the dormancy of light-sensitive weed seeds. Seed dormancy is another process that can be influenced by phytochrome, which was mentioned in relation to the control of bulbing in Chapter 4. In one experiment, dark cultivation reduced weed emergence in an onion crop by 50%, but in the next year there was no effect; the reasons for the difference were not understood (Melander *et al.*, 2005).

ARTHROPOD PESTS

The majority of arthropod pests of alliums are insects, but there are also some mites. Some of these pests damage a wide range of crops. For example, cutworms – soil surface-dwelling caterpillars of certain moths, which eat through the bases of crop plants, sometimes demolishing row upon row of young plants. Other pests are more specific to alliums and are highly adapted to locating and parasitizing them; most emphasis will be placed on these allium specialists here. The pests of alliums were comprehensively reviewed by Soni and Ellis (1990), and they give an extensive bibliography of original research. More recently, Lorbeer *et al.* (2002) have reviewed the literature on monitoring and forecasting of allium crop pests.

The number of severe pests is small and it is important to realize that pest numbers are kept in check by a wide range of diseases, predators and parasites, and that many of the latter two control agents are themselves insects or arachnids. Therefore, insecticidal chemicals should be targeted as specifically as possible at pests, to minimize the damage to beneficial species. Insecticides should be applied when monitoring or predictions based on knowledge of pest biology show a build-up of economically damaging numbers. Use of insecticides should be complementary to other techniques of pest control, including cultural methods, resistant cultivars and the introduction or encouragement of natural enemies.

This is illustrated by the 'integrated pest management' (IPM) methods used to control thrips, onion fly and leek moth described below. Resistance to many insecticides has developed in thrips and onion fly, the two most important allium

pests, and this has given impetus to the more judicious use of insecticides within a context of IPM and 'resistance management'. Pest invasion can also be prevented by covering crops with insect-excluding netting or non-woven translucent fabrics, but this is expensive and labour intensive and only likely to be economic on 'organic' crops sold at a price premium.

Onion thrips

The most damaging pests worldwide are the insignificant-looking thrips or thunderflies. These are slender insects, only about 2 mm long as adults. They are found wherever alliums are grown, but are most severe in the warmer production regions. Thrips belong to the order Thysanoptera family Thripidae. Soni and Ellis (1990) list seven species of Thripidae as allium pests, the most important of which is *Thrips tabaci*, the onion thrips, which attacks all the edible alliums. The western flower thrips, *Frankliniella occidentalis*, is also an important onion pest in the south-west of the USA. These small insects concentrate between the young leaf blades at the top of the neck. In this sheltered part of the plant they rasp and pierce leaf cells and feed on the sap released. The resultant air spaces in the leaf cells give the foliage a silvery appearance (see Plate 3a).

Large numbers of thrips can cause extensive damage to leaves, and also to flowers in seed production. Damage is most severe when plants are water-stressed in hot, dry weather. In these conditions leaf expansion is slow and increase in thrips numbers is rapid. Heavy rainfall or sprinkler irrigation can wash many thrips off leaves and increase their mortality. For example, in a dry year in New Zealand thrips populations peaked at 500 per plant on untreated onions whereas in the following year, which was wet, the peak population was 70 per plant (Workman and Martin, 2002). In Oregon, USA, leaf damage from thrips can reduce total yields by up to 27%, and the percentage of the most valuable large bulb grades to a much greater extent (Jensen *et al.*, 2003).

In the 1990s the thrips-vectored iris yellow spot virus (IYSV) emerged as a potentially devastating disease of onion bulb and seed crops (see Viral Diseases, below), particularly in the south-western USA. The severity of this disease correlates with thrips populations, and control of thrips is the best way to reduce IYSV infection (Jensen, 2005). In leek crops, thrips larvae populations must be kept below about five per plant to ensure that the majority of the crop is in the top two quality grades at harvest. Populations in excess of 15–20 per plant can cause so much visible damage that the crop will be downgraded to unmarketable under current European quality standards (Theunissen and Schelling, 1997). Thus, the disfiguring effect of thrips symptoms on leaves assumes particular importance for the quality of allium vegetables harvested green like leeks, salad onions and bunching onions, and very low pest levels must be maintained to prevent total economic loss even though losses of weight yield may be slight.

Female thrips lay about 80 eggs, which they oviposit into the leaf tissue at the top of the pseudostem where new leaves emerge. Here, the newly hatched nymphs are protected and relatively free from predators. The insects develop through two larval (nymphal) stages to the pupal stage. All stages are of similar slender shape, but the larval stages are pale yellow or green, whereas the adults are darker and have narrow, hair-fringed wings. At the end of the second nymphal stage the thrips move into the soil near the base of the plants and go into the pupal phase. The winged adults emerge from the pupae and act as the dispersal stage, the delicate insects being easily carried by wind. Nymphs are heavier and more localized feeders than adults and favour particularly young leaves emerging from the pseudostem, thereby disfiguring the elongating leaves and reducing photosynthetic capacity. The insects can remain quiescent in soil or litter in the adult or larval stages, and may also survive the winter in the necks of infested plants or bulbs.

As with so many processes in crop science (see Chapter 4), the rate of thrips development is a near linear function of temperature above a base temperature, T_b (see Fig. 5.7). From this relationship the thermal time for the development of a thrips generation from egg to adult can be quantified. *Thrips tabaci* from England required 261°C-days above a T_b of 5.9°C. Strains from warmer regions appear to have a higher base temperature and lower day-degree requirement; for example, a T_b of 11.5°C and a thermal time of 179°C days was required for thrips from onions in Texas, USA (Stacey and Fellowes, 2002). Hence, the duration of the life cycle decreases as temperature increases and, at 30°C, it takes only 10–11 days from egg to adult. As a consequence there are more generations per year in warm climates. In the Treasure Valley onion growing area of Oregon, USA there are five to seven generations per year (Jensen, 2005), whereas three generations per year are typical of Belgium (de Clercq and van Bockstaele, 2002).

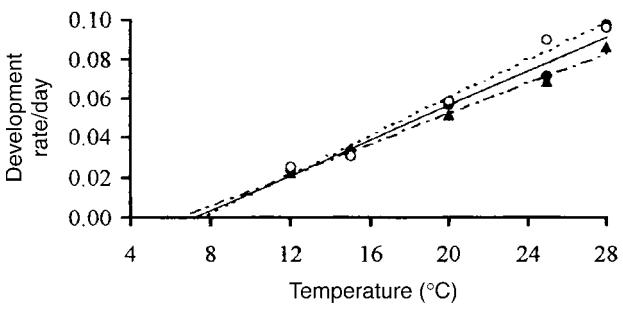


Fig. 5.7. The relationship between mean development rate and temperature for *Thrips tabaci* from York ●, Cambridge ▲ and Surrey ○ in the UK (from Stacey and Fellowes, 2002. Courtesy of the *European Journal of Entomology*).

Thrips are usually controlled by insecticidal sprays and, in a bulb onion crop, two or three sprays of an effective insecticide when pest populations are likely to increase can give adequate control (Richter *et al.*, 1999; MacIntyre Allen *et al.*, 2005). Onion thrips have many alternative hosts, and the timing of invasions can vary with the neighbouring vegetation – in particular, nearby crops and crop operations. Consequently, thrips infestations are not as easy to predict using day-degree models as are invasions of the onion fly or leek moth, where the host range is restricted to alliums.

To avoid unnecessary spraying, 'scouting' systems have been devised in several countries to determine when thrips populations in allium crops are building up to a threshold level that warrants control (Richter *et al.*, 1999; Lorbeer *et al.*, 2002; Jensen, 2005). Scouts need to be trained in standard procedures in order to obtain reliable results. For example, in German trials fortnightly samples of five plants from each of ten positions in a field were simply scored for the presence or absence of thrips, and insecticide was applied if more than 50% of plants contained thrips (Richter *et al.*, 1999). The data showed that a 50% plant infestation score corresponded to an average of about three thrips larvae per leek plant and just 2% of damaged leaf area, which is acceptable for good-quality leeks. Adoption of spraying according to this scouting system in Germany reduced insecticidal application for thrips control in onions by 60% and in leeks by 30%, without compromising quality or yield.

To try to understand better the reasons for local and seasonal fluctuations in *T. tabaci* attacks, a model has been developed that combines within-farm, small-scale geographical information on vegetation patterns, including crop layouts, along with temperature-driven (e.g. Fig. 5.7) dynamic simulations of thrips development and migration (Booij, 2003). The aim is to understand how local differences in agroecosystems lead to the between-farm variations in thrips damage that occur.

In many allium-producing regions growers have noticed a decline in the effectiveness of insecticides for thrips control because of the evolution of resistance in the local populations. Onion thrips resistance to both pyrethroid and organophosphorus insecticides has been reported in many regions (MacIntyre Allen *et al.*, 2005). To maintain acceptable control, growers frequently respond by increasing the dosage and frequency of treatments until the pest becomes totally resistant (Theunissen and Schelling, 1999). When a new insecticide is introduced it is important that its use is rotated with insecticides with a different mode of action, even if they are not as effective, to avoid continual selection pressure for resistance to the novel chemistry and a repeat of the familiar 'boom and bust' pattern in insecticide effectiveness. Ideally, such 'resistance management' occurs within a wider context of IPM, which could include the thrips scouting described above to avoid unnecessary sprays and cultural controls like maintaining the plants well-watered, which reduces the impact of thrips damage. In addition, sprinkler irrigation can directly wash many thrips off onion leaves.

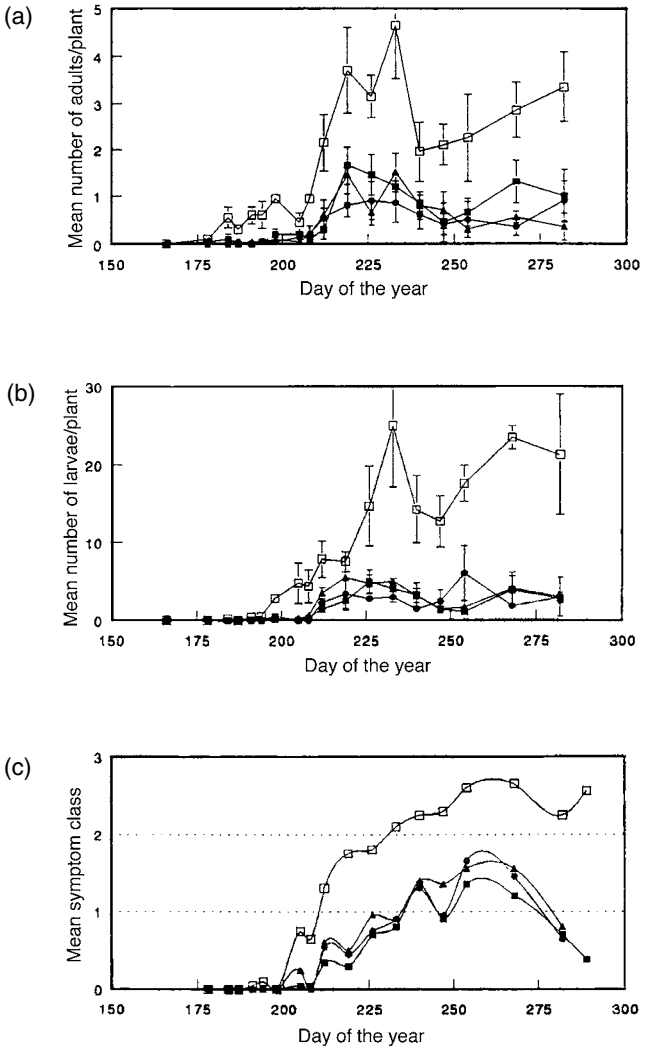


Fig. 5.8. The effects of undersowing leeks with subterranean clover on the numbers on the leeks of adult thrips (a), thrips larvae (b) and the mean thrips damage symptom class (c) of the leeks. Clover was sown in mid-April and the 22.5 m^2 leek plots were planted in mid-June. Clover was mown when it exceeded 15 cm in height. Leeks of symptom class 2 and above are of unacceptable quality for European markets. □, Monocropped leeks; ■, undersown plots adjacent to monocrop plots; ▲, undersown 30 m distant from monocrop plots; ●, undersown 60 m distant from monocrop plots (bars ± standard error) (from Theunissen and Schelling, 1999. Courtesy of the *International Organisation for Biological Control Bulletin*).

Choice of variety can also help. In the western USA, 'Spanish-type' onion cvs with shiny bright green foliage are generally less susceptible to thrips damage than are onions with grey/green foliage (Jensen, 2005). Resistant varieties produce leaves widely separated on the pseudostem and have a wide angle of divergence between the leaves emerging from the neck, thereby minimizing the shelter for thrips between leaves. Ploughing to bury overwintering thrips in soil or on crop debris will reduce the infection source for the following year. Overwintering leek or onion crops are likely to act as a 'green bridge' for overwintering thrips, and situating spring sowings or plantings remote from these may delay infestation.

IPM principles are embodied in the use of 'soft' insecticides like Spinosad, which control plant-eating pests but cause little damage to the predatory arthropods that help to keep pest numbers in check (Williams *et al.*, 2003). Experiments in Oregon in which Spinosad was applied to bulb onion crops that were also mulched with straw gave better control of thrips and significantly higher yields and monetary returns than those treated with the usual insecticide schedule (Jensen, 2005). Populations of thrips predators under the Spinosad/straw treatment were almost four times those under the standard insecticidal treatment, and increased predation may have supplemented the insecticidal effect of Spinosad to produce the high level of pest control. Reduced thrips damage had previously been noted on onion fields mulched with straw to improve irrigation infiltration, and similar benefits have been observed in trials of straw-mulching on leeks (Weber *et al.*, 1999).

Undersowing or intercropping allium crops with another species offers a more radical potential solution to thrips control. Numerous experiments have shown that leek crops undersown with clover do not suffer much thrips damage compared with normal monocrops (see Fig. 5.8; Theunissen and Schelling, 1999). Leeks intercropped with carrots also have much lower thrips populations (Legutowska *et al.*, 2003). The reasons for this effect are not fully understood, but there is evidence that the females of pest insects do not oviposit until they have made several successive landings on leaves of a suitable food crop. If an acceptable species is intermingled with a non-host species, the female may not receive sufficient stimulus to oviposit and usually departs the crop without laying eggs (Finch and Collier, 2000).

However, when pots of leek plants that had been grown with clover undersown but from which the clover leaves had been mown off were placed in a thrips-infested field, only about one-third the number of adult thrips were found on these plants as were found on potted leeks grown without clover (den Belder *et al.*, 2000). This experiment indicates that something other than the visual, olfactory or chemical signals that thrips detect from adjacent clover leaves makes the undersown leeks less attractive to thrips than leeks grown in bare soil. Experiments have established that neither increased predator levels nor decreased nitrogen content in undersown leeks can explain this suppression of thrips. Some physiological change in leeks brought about by

competition from the undersown or intercrop species has been postulated to inhibit thrips feeding and development.

Unfortunately, undersowing with clover slows leek growth and reduces total yield, even though crop quality is improved because of less thrips damage (Weber *et al.*, 1999). However, by sowing the clover only between the rows of transplanted leeks, competition was reduced and leek yields almost equal to those attained in bare soil were attained. Ninety nine per cent of the leeks from this undersowing treatment were marketable, 89% in the best-quality grade, whereas from bare soil only 44% were marketable with just 1% best quality (Theunissen and Schelling, 1998). Therefore it may be possible to refine undersowing or intercropping systems so that the benefits of reduced pest (and disease) pressure are gained without much loss of yield, or possibly, with intercropping, with a gain in overall financial return per unit area.

These techniques are not yet used in practice. This may be because more development work is needed to optimize suitable systems (see Fig. 5.4). However, they are inevitably more complex than monocropping and would require more husbandry skill. Also, as described in Chapter 4 and as illustrated by leek–celery intercropping experiments (see Fig. 5.4), alliums are weak plant competitors and it will be difficult to devise systems where they are not severely suppressed by their intercrop, although carrots are fairly slow growing, not highly competitive and can occupy the ground for a similar period to leeks, so this could be a commercially viable system for leek production, requiring little or no insecticide.

Onion fly or maggot

The onion fly or onion maggot, *Delia antiqua*, is one of the 22 species of two-winged flies (Diptera) listed as pests of alliums by Soni and Ellis (1990). The onion fly is a specialist feeder on alliums, and attacks all the vegetable alliums. The most severe damage is caused by the maggots burrowing into the base of seedlings in the spring, causing wilting and collapse. When seedlings die, the maggots migrate to neighbouring plants and may destroy successive plants in a row, resulting in gaps in the crop (see Plate 3b). Similar damage to young allium crops is caused by *D. platura*, the bean seed fly or maize seed maggot, which normally attacks spring-sown crops a week or two before the onion fly. *Delia platura*, which looks very similar to the onion fly, has a much wider host range. In many onion-growing regions there are three generations per year of the onion fly. Maggots of the second and third generations burrow into the bases of large plants and developing bulbs and thereby predispose them to rotting by secondary infections of fungi and bacteria (see Plate 3c).

Adult onion flies are 8–9 mm long, grey and resemble the common housefly. The females lay eggs in soil near the base of allium plants. The larval stage is the damaging maggot, which is dirty white and grows to 8 mm in

length. The fully grown larvae migrate to a depth of about 6 cm in the soil, where they develop into brown pupae. Under both low winter temperatures and high summer temperatures the insect can enter a state of developmental arrest, termed diapause, in which it is able survive extremely low or high temperatures. Low temperatures and short photoperiods or high temperatures and long photoperiods, respectively, initiate the sequence of physiological changes that lead to winter or summer diapause (Bin Chen *et al.*, 2005). The pupae remain in diapause during winter or during hot summer periods, following which development resumes and adults emerge to mate and lay the eggs of the next generation.

In spring, the year's first-generation adults emerge in fields that grew the previous season's allium crops, and they must locate the new season's allium fields to lay their eggs (oviposit) near host plants suitable for larval development. Initial dispersal appears to be random in direction but, after a period of reproductive maturation, the flies become responsive to volatile chemicals characteristic of alliums (see Chapter 8). At this stage the flies are highly attracted to dipropyl-disulfide (Pr_2S_2), one of the volatiles that onions can produce, and they will fly upwind towards traps baited with Pr_2S_2. Electrical signals detectable from onion fly antennae when exposed to Pr_2S_2 indicate that it is a strong olfactory stimulant (Gouinguene *et al.*, 2005).

Having located the source area for the odour they use visual cues to land preferentially on vertical, green, cylindrical surfaces that mimic the form of allium plants. These responses suggest that ovipositional host-finding by female onion flies is dominated by olfactory responses at long range and by visual cues at short range (c. 1 m) (Judd and Borden, 1991). Having alighted, females exhibit different behaviours on different-shaped surfaces. On narrow (8 mm diameter) vertical cylinders they show a characteristic pattern of movement and frequently go on to oviposit near the base of the cylinder. The number of eggs laid near the base diminishes with increase or decrease in cylinder diameter and when the cylinder/substrate angle deviates from 90° (Harris and Miller, 1984). Female flies oviposit maximally in a substrate at about 20°C, a temperature that also favours egg survival and development (Keller and Miller, 1990).

Insecticides applied in the furrow when seeds are sown can give very effective control of onion fly. Ritcey *et al.* (1991) showed that an in-furrow active ingredient rate of 2.2 kg/ha of organophosphorus insecticides – among them chlorpyrifos and fonofos – was sufficient to control the first- and second-generation onion maggots on organic soils in Ontario, Canada. The insecticides were absorbed by onion seedlings but were concentrated in the roots and skin and, by the time of bulb harvest, insecticide residues in the bulbs were undetectable.

Similar levels of control have been achieved with even less active ingredient (AI) per ha by film-coating seeds with insecticide before sowing. Experiments on organic soils in New York State, USA showed that film-coating onion seeds with cyromazine at a rate of 50 g AI/kg seed reduced seedling losses from onion fly to negligible levels (Taylor *et al.*, 2001). By applying the insecticide as a

seed-coating, control was achieved with only 15% the AI/ha needed for an equivalent in-furrow treatment. The low insecticide doses needed when using seed-coating minimize the risks associated with insecticide contamination, including the destruction of beneficial insects and the exposure of field workers to toxic substances during in-furrow treatments.

Aerial sprays of insecticides are also used to destroy egg-laying females. By monitoring the insects caught in traps, it has been possible to restrict spraying to periods when egg-laying adults are infesting onion crops (Lorbeer *et al.*, 2002). The traps are made of highly reflective white, yellow or blue sticky plastic sheets baited with volatile attractants like Pr_2S_2 (see above). Using these IPM techniques, the number of sprays in Ontario was reduced from around ten per season to just two. The time to start monitoring can be determined from temperature records and knowledge of thermal time requirements for egg-laying adults to develop (see Table 5.2).

This predictive system was found unsatisfactory for Germany, and a more complex model has been developed that predicts the progress of cohort insects through each developmental stage until the egg-laying adults are in flight (Otto and Hommes, 2000). This model was based on the relationships between temperature and development rate shown in Fig. 5.9, with pupal development arrested by diapause (see above) if mean soil temperatures are below or above specified limits at the appropriate times of year. The model specifies that flight activity of adults is maximal at mean wind speeds of 3 m/s and below, and declines linearly to zero with increasing mean wind speeds between 3 and 8 m/s.

Predictions of adult fly infestation in the two main chive-growing regions of Germany corresponded fairly well with monitored populations for the first two of the annual generations, but accumulated errors made the prediction of the third generation unsatisfactory. The model was entered for further testing within a suite of computerized decision aids for plant protection used by the German crop extension services.

Soni and Ellis (1990) have reviewed the additional aspects of control that are important within an IPM strategy. These include the destruction of infested

Table 5.2. The thermal time above a base temperature of 4.4°C needed to complete the development of each life stage of the onion fly, *Delia antiqua*, in Ontario, Canada (from Liu *et al.*, 1982).

Life cycle stage	Thermal time needed (°C days)
Egg	50
Larva	287
Pupa	306
Adult, pre-egg-laying	103
Generation time (egg to egg)	746

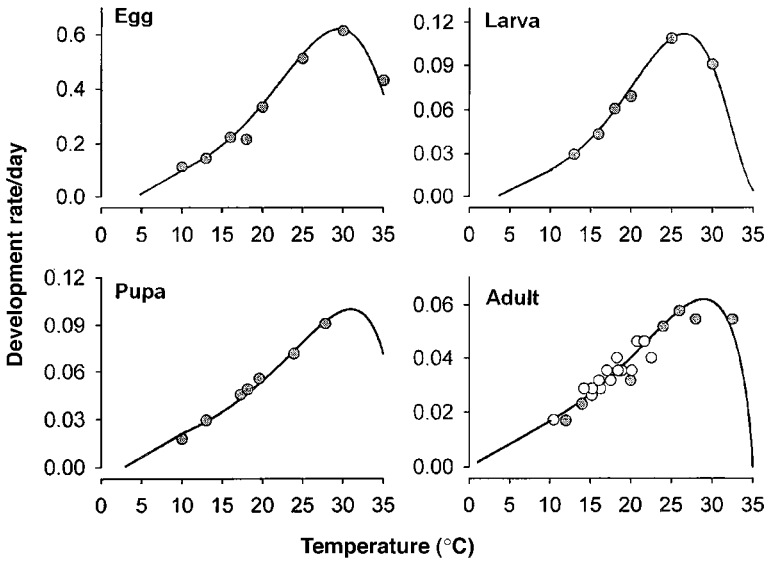


Fig. 5.9. Relationships between temperature and development rate for the four life stages of the onion fly *Delia antiqua*; shaded circles represent data from constant temperature experiments, and open circles from fluctuating temperatures. The lines are derived from equations fitted to the data (from Otto, 2002, Fig. 26).

debris, the mutual isolation of onion, garlic and leek fields and a 2- (or more) year rotation between allium crops. Numerous predators and parasites of *D. antiqua* have been identified, including fungal pathogens and nematode parasites, and these are important particularly in reducing numbers in the second and third annual generations. The insecticide cyromazine, which is now approved for use as a seed-coating (see above) on onions in the USA, is highly effective against diptera like the onion fly, but is relatively non-toxic to other insects, including beneficials (Taylor *et al.*, 2001).

Cultivars differ in their content of the precursors of volatiles and in their colonization by non-pathogenic, surface bacteria that increase volatile emission. Decreases in these factors have been shown to correlate with increased varietal resistance to fly attack. However, egg-laying preferences may not be so important if flies are presented with one such 'resistant' line rather than with several lines differing in volatile production. To reduce volatile production by plants in the field, and thereby their attractiveness to egg-laying females, plant damage during cultivation and herbicide application should be minimized. IPM has become important for onion fly control because past practices – including routine spraying and the continuous cropping of onions on the fertile 'muck' soils of New York and Ontario and elsewhere – have led to

the evolution of resistance to many insecticides, including chlorpyrifos (see above).

Another interesting control technique was developed for onion fly during the 1970s (Soni and Ellis, 1990). Adult onion flies were raised in culture, sterilized using radiation or chemicals and then released into onion crops in large numbers to mate with – and thereby reduce the fertility of – wild populations. Reductions in the reproductive rate of the pest resulted, and the technique has been used commercially in The Netherlands. This 'sterile male' technique had previously been successful in the control of other insect pests.

Other dipterous pests

Certain *Eumerus* spp., bulb flies, tunnel into allium plants and can reduce bulbs to a rotten mass. The maggots are difficult to control when inside plants, and infested bulbs should be destroyed. Spraying of plants and the dusting of bulbs with insecticides are used in control.

Leaf miners, *Liriomyza* spp., are small flies that lay eggs on allium leaves in the spring. The larvae mine through the photosynthetic tissue, and severe infestation results in leaf collapse (see Plate 4a). The flies pupate in soil. The flies have more generations per year the warmer the climate. In central Europe these are a severe pest. Eleven species have been reported as damaging alliums, with *L. nietzkei* and *L. cepae* being confined to these crops. Many insecticides are effective for control. In the early 1990s the leaf mining fly *Napomyza gymnostoma* emerged as a disfiguring pest of chives and leeks in Austria. It has two generations per year, one in spring and one in autumn. A monitoring and warning service for the pest was started in that country in 1997. It can be controlled by organophosphorus insecticides applied when larvae are in the upper parts of the leaves (Kahrer, 1999).

Leek moth

Acrolepiopsis assectella, the leek moth, is a severe pest of leeks in western Europe, also attacking onion, garlic, chives and shallots (see Plate 4b). Damage is caused by caterpillars mining within the leaves and later in the central crown of the plant, where they create a cavity, destroy young leaves and predispose the plants to rotting by secondary pathogens. Leek moth attack can completely destroy young plants and seriously downgrade the harvest quality of older plants. The caterpillars also damage seedheads and can destroy the seed crop.

Adult moths are brownish grey, with a 17 mm wingspan. Females lay up to 200 eggs singly or in small groups near ground level on leeks and other alliums. The yellow-green caterpillar grows to 13 mm, and ultimately weaves a cocoon for the red-brown pupa on dead vegetation near the host plant, or

among its seed stalks. The insect may overwinter as an adult or a pupa, and control is aided by deep ploughing to bury and destroy the pupae, or by frequent cultivation to expose them to predators.

Adults become active in egg-laying when mean temperatures exceed 10–12°C. In France, where the moth is a severe pest, up to five generations occur per year in the south, and systems for integrated control have been developed. The number of generations per year depends on temperature, with three being normal in Germany and just two in the UK. Models based on day-degrees can predict rate of development, and hence when egg-laying adults will be flying. Adult emergence and numbers are also monitored using traps baited with (2)-11-hexadacanal. This is a volatile chemical (pheromone) produced by the female moth that attracts males. The information gathered is used to time the application of insecticides in relation to when the moths are laying eggs. In Germany, two applications of deltrathrin, a synthetic pyrethroid insecticide with some residual activity, applied 3 weeks after the beginning of egg-laying, gave excellent control (Richter and Hommes, 2003).

Studies of behaviour and the electrical responses of antennae on leek moth adults exposed to the volatiles derived from the alk(en)yl-cysteine sulfoxide precursors found in leeks and other alliums (see Chapter 8) have shown that the moths locate allium plants for their egg-laying using these olfactory signals (Dugravot and Thibout, 2006). When leeks are attacked by leek moth larvae, they increase the quantity of the alk(en)yl-cysteine sulfoxide precursors produced and, as a result, more volatiles are produced by leeks subject to leek moth attack than by plants that are simply injured mechanically (Dugravot *et al.*, 2005).

One of these volatiles, dimethyl disulfide (DMDS), has been shown to be a powerful neurotoxin for non-adapted insects (Dugravot *et al.*, 2003), and the sulfur volatiles function as a defence against non-adapted plant-feeding insects. For leek moth larvae, however, the higher level of volatiles in leeks under their attack is not lethal, but it does lead to a slower development rate in males and about a 20% reduction in egg-laying potential in females (Dugravot and Thibout, 2006). Furthermore, DMDS is a powerful attractant for the wasp *Diadromus pulchellus*, which is the main parasitoid of leek moth larvae. DMDS is produced by particular bacteria in the frass of leek moth larvae (Thibout *et al.*, 1995). As a consequence, the parasitic wasps are more strongly attracted to leeks damaged by leek moth feeding than to undamaged or mechanically damaged leeks. These findings suggest a complex defence system against leek moth involving four trophic levels: the plant, the pest, the frass bacteria and the parasitoid. The increase in volatile precursor production following the pest attack directly reduces the reproductive capacity of the developing larvae, but it also has an indirect effect in attracting more parasitoid wasps. The combined effect may be to reduce the numbers of second-generation pests (Dugravot and Thibout, 2006).

The leek moth is one of the 20 species of moths – including several cutworms – listed as allium pests by Soni and Ellis (1990). In tropical regions the beet army

worm, *Spodoptera exigua* can be a serious pest (Lorbeer *et al.*, 2002). The pest is protected from contact insecticides when inside the hollow leaves of shallots and is therefore difficult to control. Beet army worm-resistant shallots that produce *Bt* toxins have been developed by genetic transformation (see Fig. 3.7b).

Shallot aphid

Myzus ascalonicus, the shallot aphid, is one of 18 species of the order Hemiptera, plant bugs and aphids, reported as allium pests. It may infest onion bulbs in store, where it damages fleshy scales and distorts developing leaves and flower parts. It and other aphids – for example, *M. persicae* – can transmit many viruses of alliums, including onion yellow dwarf (see Viral Diseases). Quick-acting insecticides must be used if they are to have any preventative effect against virus transmission. Fumigation with nicotine or pirimicarb has been used to control aphids on stored bulbs.

Other pests

Twenty-three beetles, order Coleoptera, were reported as allium pests by Soni and Ellis (1990). Many affect stored bulbs but some destroy foliage. They also reported nine species of mites, class Arachnida, order Acarina, as pests. Mites feed on sap released after piercing plant cells, and some enshroud the plants in a characteristic web. Allium pests include red spider mites, *Tetranchyus* spp., which damage many crop species, and also *Aceria tulipae*, the garlic mite. This tiny mite, only 0.10–0.25 mm long, can infest stored bulbs of garlic, onion and shallot, causing shrivelling. Infested growing plants develop yellow-streaked, twisted leaves. This is termed tangle-top malady in India. The mite is a vector of garlic mosaic and onion mosaic viruses (see Viral Diseases). Control is difficult, since the pests lie hidden between leaves in the neck, or are inaccessible in bulbs. Organophosphorus acaricidal sprays are used for control on growing plants.

NEMATODE PESTS

Nematodes, or eelworms, are small, unsegmented worms which form an important constituent of the soil fauna. Sixty-eight species identified as associated with the roots of crop alliums were listed by TDRI (1986). A small percentage have been shown to be damaging pests and one species, the stem and bulb eelworm, *Ditylenchus dipsaci*, is a major pest. Green (1990) wrote a detailed review and bibliography of the nematode pests of alliums, and Perry and Moens (2006) include more recent information.

Root parasites

Apart from the stem and bulb eelworm, the pest species attack root systems. These root parasites can be categorized as either ecto- or endoparasites and also as either sedentary or migratory. The ectoparasites feed on the outside of the root systems, whereas endoparasites feed internally. The migratory species destroy plant tissue as they feed and continually move to invade undamaged roots. The sedentary species induce localized growth modifications in roots, and these function as long-term nutrient sources for the parasite.

The damage caused by all these root parasites is similar. Basically, the attenuation of root growth impairs the potential for water and nutrient uptake, and this predisposes plants to water or nutrient stress and, as a result, growth rates are reduced and the attainment of a given plant weight is delayed, usually leading to a lower yield at the end of the growing season (Schomaker and Been, 2006). The degree of damage varies with a number of factors, including the population density of the pest in the soil and temperature. The size of the plant is important; as with most disorders, small seedlings are more vulnerable than larger plants with more extensive root systems.

It is common to protect seedlings by applying a granular nematicide, like aldicarb, along the drilling line at sowing, thereby protecting the young seedlings and allowing plants to become established. Soil sterilization using methyl bromide, or an overall application of nematicide, frequently increases yields. However, these substances are highly toxic, treatment is expensive, and re-invasion by the pests can be rapid and populations may then rise above their original level. In warm, sunny countries nematodes, along with other soil-borne pests and pathogens, can be controlled by soil 'solarization'. This is the sterilization of the upper layer of soil as a result of solar heating, following wetting and sealing under a tightly stretched layer of clear polyethylene. Again though, pests are likely to reinvade from deeper, cooler layers of soil and the control will need to be repeated. Some of the pest species have a narrow host range, and their numbers can be reduced by including non-susceptible crops in the rotation. However, many of the pest nematodes have a wide host range and control by crop rotation is impractical.

Stem and bulb eelworm

The stem and bulb eelworm, *Ditylenchus dipsaci*, is an extremely serious pest in temperate climates and at high elevations in tropical regions. It is difficult to control once established. There are many strains of *D. dipsaci* indistinguishable by appearance, some specific to a particular host plant species and some with a wider host range (Duncan and Moens, 2006). It has so far been difficult to distinguish races, even using molecular techniques, and this complicates management using crop rotation or resistance. Unlike the other pest nematodes,

D. dipsaci proliferates in shoots and causes them to become twisted and distorted, with shortened leaves and multiple side shoots, a condition termed 'bloat' in onions (see Plate 4c). Pimple-like spots termed 'spikkles' also distort the shoots of infected onions and garlic. Young seedlings are killed after the cotyledon swells and collapses, and older plants may die if leaf bases are severed. Invasion by nematodes increases secondary damage due to bacterial decay. Lightly infested bulbs are likely to develop bacterial decay in storage, which shows as brown, necrotic 'rings' corresponding to the infested scales. Therefore, even a low proportion of plants attacked is serious in onion or garlic grown for storage, since rotting makes the infected plants worthless.

The nematode invades through cracks in the outer sheaths below ground level. There are four juvenile stages and the one adult stage. The pre-adult stage is normally the migratory, infective stage. The life cycle lasts about 3 weeks and the pest multiplies rapidly. The life cycle may be completed within a plant, or it may involve migration to other plants. Within the plant the nematodes secrete enzymes that dissolve pectin, causing cells to separate, thereby softening plant tissues and enabling the nematodes to spread. The loosened cells are susceptible to bacterial rot. The nematodes also secrete plant growth regulatory chemicals that inactivate auxin, and which promote abnormal cell division and enlargement. The distorted 'bloat' symptoms of infested plants can be simulated by damage from 'hormone type' herbicides.

The pre-adult stage is highly resistant to desiccation and tolerant of freezing, and can survive for many years without feeding in dry soil, plant debris or on seed-coats. *Ditylenchus dipsaci* survives for a relatively short time in the absence of a host in warm, moist soil. Bulbs for seed production, which are lightly infected, may survive storage and go on to produce infested flowering plants which produce seed infected by nematodes on the seed-coat. Infected seed can be an important primary source of spread of the pest, as can any vegetative propagating material. In The Netherlands, onion set production crops are inspected to ensure freedom from the pest to avoid spread in this way.

Within the field, survival and spread of the nematodes is favoured by moist clay or silt soil, and they are shorter-lived on sandy soils. They spread only about 1 m/year by migration from an infection source in ideal moist soil conditions. More serious, and a frequent cause of epidemic crop losses, is spread by surface water flooding. This can follow heavy rain on poorly structured soils that form a surface 'cap', which has a low rate of water infiltration. The result can be wide areas of devastated alliums corresponding to the flooded zones.

Control of *D. dipsaci* requires a comprehensive series of measures to prevent its introduction and to restrict its survival and spread. Seed crops should be nematode free. Any infected mother bulbs that survive storage, or mother plants showing the symptoms of infection, should be rogued from the seed crop. Nematodes can be destroyed by fumigating infected seed with methyl bromide. Onion sets, shallots and garlic cloves for planting should be grown on nematode-free land and inspected. Eradication from infected sets, shallots and

cloves is possible by immersion in hot water at 45°C for 2–3 h. Also effective is dipping in various nematicidal chemicals, either alone or in addition to hot-water treatment. Transplants should be raised using nematode-free seed and growing media.

Chemical sterilants and solarization can destroy the pest in the soil, but these treatments are expensive. After such treatments it is important to reduce the rate of spread from surviving foci of infection. The risk of surface water movement can be minimized by good drainage and soil husbandry that conserves soil structure and avoids 'capping'.

In temperate climates the nematode survives for too long on clay loams and fine silts, and has too many alternative hosts, for rotation to be a practicable control once such soils are infested. However, on lighter soils, rotations involving wheat, barley and brassicas can lower the risk to following alliums. The short persistence of the nematode in warm, moist soil makes control possible by 2–3-year rotations and soil solarization in warm climates (Duncan and Moens, 2006). Field hygiene to avoid the spread of infected waste from any of the host plants should always be followed.

Theoretical models have been developed describing how the influence on yield of nematode pests depends on their initial population density in the soil (Schomaker and Been, 2006). The effects of nematicides and host resistance on the pest population in the soil and crop losses have been modelled. The model that applies to stem and bulb eelworm, where an infected plant is totally worthless, differs from the model applicable to root parasites, where loss in yield varies continuously with the intensity of root damage.

VIRAL DISEASES

Symptoms of yellow mottling (mosaic) or striping on leaves, distortion of shoots and reductions in yield caused by viral infections can occur in allium vegetables. The viruses are sub-cellular particles consisting of a protein coat surrounding a central strand of RNA, which carries the genetic information (Agrios, 2005). The majority of viruses infecting allium vegetables are rod-shaped and flexuous (bendy), the longest being about 800 nm long × 12 nm wide. After infection, host cell replicative processes are diverted towards virus proliferation. Sometimes this disruption results in obvious symptoms in the host plant, but 'latent' viruses proliferate within the host without symptoms.

The viruses are transmitted from plant to plant by aphids, mites or thrips, depending on species, and therefore viral disease epidemiology is linked with the biology of these arthropod pests (see 'Arthropod Pests', above). Thus, virus transmission depends on the occurrence, numbers, infectivity and migration pattern of these vectors. The main viruses causing disease in allium crops have a narrow host range, primarily restricted to alliums. Fortunately they are not transmitted in seeds. These two facts make crop rotation plus crop hygiene an

effective strategy of disease control in onions and leeks. Allium viruses are transmitted by vegetative propagation, and traditional cultivars of garlic and shallot are usually chronically infected with a mixture of viruses.

Information on the viral diseases of vegetable alliums was reviewed by Walkey (1990) and, more recently, those of garlic by Salomon (2002). Much information about different isolates of these viruses can be found at the web site of the International Committee on the Taxonomy of Viruses (ICTVdB Management, 2006). Table 5.3 lists the viruses and summarizes some of their features.

There are different strains within these virus species that can differ in virulence and infection range. For example, the garlic strain of OYDV cannot infect onion, and vice versa (van Dijk, 1994). RNA sequences vary considerably between different strains of the same virus, with up to about 20% sequence variation within a species. The increasing volume of sequence information is making it possible to trace patterns of genetic divergence and affinity both between strains within a species and between species (Tsuneyoshi *et al.*, 1997; and other references in Table 5.3 concerned with RNA sequences). Scientists involved in conserving the world's heritage of vegetatively propagated alliums in gene banks are aware of the danger of introducing novel virus strains to a locality via such collections, and take steps to avoid this (Maggioni *et al.*, 2002).

Most of the viruses are symptomless and do not cause obvious disease. However, three – onion yellow dwarf virus (OYDV), leek yellow stripe virus (LYSV) and iris yellow spot virus (IYSV) – cause serious diseases. OYDV infection causes onion leaves to become flattened and crinkly, with yellow striping or complete yellowing of leaves. Infected leaves bend and lie along the ground. Bulbs from infected plants are smaller and have a shorter dormancy than healthy bulbs, and yield losses of up to 60% have been recorded. Infection also reduces the yield of seed crops. OYDV has been reported in most onion-producing areas. OYDV also produces severe disease symptoms in shallot and garlic.

LYSV infection causes leek leaves to be yellow striped and flaccid, so that leaves are downturned and trail along the ground. Yield losses of up to 54% can occur, and infected plants have reduced frost hardiness and a shorter shelf-life after harvesting. Shallot latent virus (SLV) is found in virtually all shallots and can infect the other allium crops. The influence of SLV on shallot yield, if any, is not known but, if SLV is present along with LYSV in leeks, the severity of disease is increased.

OYDV, LYSV and SLV are transmitted on the mouthparts of aphids on short probing visits from plant to plant. Insecticides are not sufficiently fast-acting to prevent spread in this way from infected plants. Therefore, disease prevention depends on the elimination of infection sources. Fortunately, these viruses are not transmitted in seeds, and therefore crops raised from seed are initially virus-free. Also, the host range of these viruses is restricted to alliums. Hence, if crops are raised from seed and isolated from infected alliums that act as a virus source, these diseases can be avoided. LYSV built up to epidemic levels in The Netherlands and Belgium in the 1970s when year-round leek production became common.

The infection sources for spring-planted crops were overwintered diseased plants. By introducing a time gap in the annual production cycle, so that newly planted crops were not contemporaneous with older, infected crops, the transmission cycle for the virus was broken and the disease was controlled. The same strategy has successfully controlled OYDV in several areas. The removal of any diseased 'volunteer' plants remaining from previous crops is important, and crops should be 'rogued' early in the season to remove any viral plants that might act as a disease source. Also, leek and onion seedling production and drilled crops should be isolated from virus sources in shallots, garlic and overwintering infected alliums in home gardens. Onion sets must be raised in isolation from infected plants and must be monitored during production for freedom from virus.

The lack of alternative hosts showing differential susceptibility to, and transmission of, the different component viruses in the mixtures found in garlic made it difficult to identify the species in the mixture by the traditional methods of plant virology. Most of the viruses are flexuous rods and look similar under the electron microscope; several are transmitted by aphids, so these features could not resolve the mixture. In the 1970s virologists in The Netherlands distinguished OYDV, LYSV and SLV as separate viruses, and prepared antisera that reacted specifically with the coat proteins of the purified viruses. These antisera made it possible to use ELISA and immunosorbent electron microscopy (ISEM) to identify and distinguish these viruses (Walkey, 1990).

More recently, molecular methods have been applied to determine the sequence of bases in the RNA (i.e. the genetic code) of most of these viruses (Salomon, 2002; ICTVdB Management, 2006). The number of bases in their RNA strand ranges from 8363 for Garlic Virus X to about 17,500 in the Tospoviruses. The genetic codes were the basis for developing the technique of reverse transcriptase-polymerase chain reaction (RT-PCR) identification of allium viruses (Salomon, 2002). This involves separating the RNA from infected plants and making DNA complementary to the RNA using the reverse transcriptase enzyme. Short 'primer' sequences of DNA specific and diagnostic for the complementary DNA of each virus have been designed, based on their genetic codes (Salomon, 2002). If a virus is present, its primers initiate the amplification of its complementary DNA many-fold in the PCR reaction, and diagnostic bands of amplified DNA can be separated and identified by electrophoresis (see Fig. 5.10). In this way the presence or absence of particular viruses in a complex mixture can be determined (Tsuneyoshi and Sumi, 1996; Takaichi *et al.*, 1998). RT-PCR can be up to 10,000 times more sensitive than ELISA for garlic virus detection (Salomon, 2002; Lunello *et al.*, 2005).

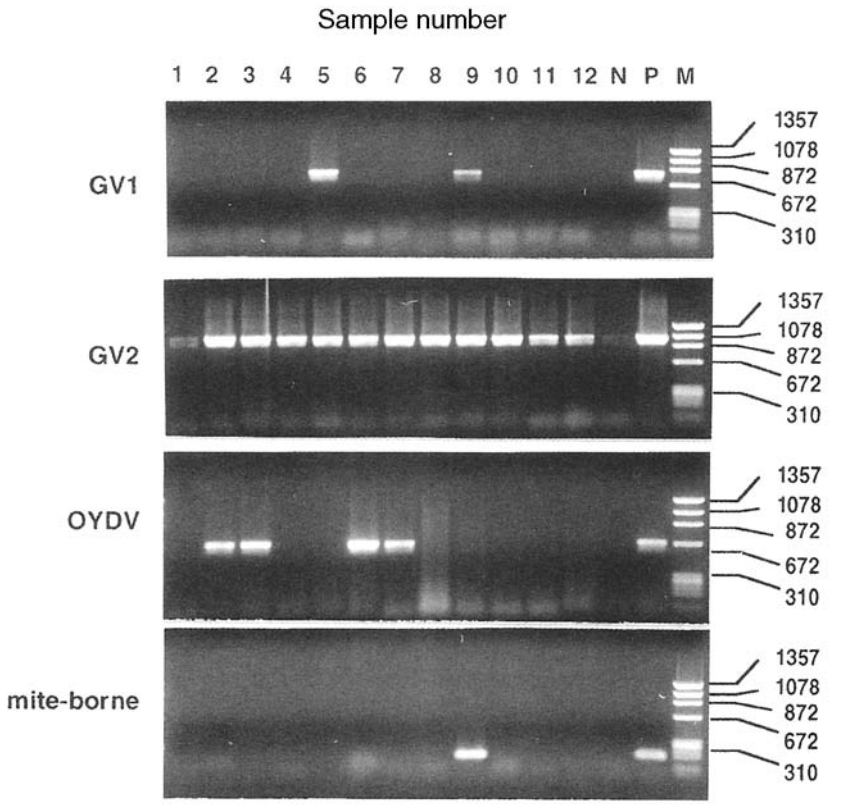
Thanks to these immunological and molecular methods it has been possible to distinguish the different viruses in Table 5.3 and make rapid progress in determining the component viruses causing what, for many years, was simply called 'garlic mosaic' disease.

In France, a long series of investigations has been aimed at overcoming the problem of garlic mosaic (Messiaen *et al.*, 1993). Systematic observations of

Table 5.3. Viral diseases of allium vegetables.

Code	Name	Genus[a]	Host range[b]	Symptoms	Yield decreases	Vectors	Other information
OYDV	Onion yellow dwarf virus	Potyvirus	O, g, s[2], j, w, r[3]	Systemic leaf striping; curling of leaves and scapes; stunting; mosaic on g	Large, 40–60% in g depending on cv.[4]	Aphids	Different strains in o & g
LYSV	Leek yellow stripe virus	Potyvirus	L, g, o	Yellow leaf striping	17–54% in g, varying with cv.[4]	Aphids	Different strains in o & g
SYSV	Shallot yellow stripe virus (Welsh onion YSV a strain[5])	Potyvirus	S, o, j, w, r	Systemic yellow striping		Aphids	S, j or w strains differ in species infectivity range[5,6]; nt[c] sequence more like OYDV than LYSV[7,8]
SLV	Shallot latent virus	Carlavirus	S, g, o, l, j, cl, r[1]	None obvious[2]		Aphids	GLV, garlic latent, is a strain of SLV – shown by nt sequence[9] and antiserum reactions[10]
GCLV	Garlic common latent virus	Carlavirus	G, l, ghg[1]	None obvious[10]		Aphids	Nt sequence distinct from SLV[9]
GarV-A,B,C,D, E,X[11]	Garlic virus A, B, etc.	Allexivirus	G		GarV-A, 14–30%; GarV-C, 0–15%[11]	Mites (*Aceria tulipae*)	Nt sequences of A,C[12] and X strains[13,14]
SVX	Shallot virus X (onion mite-borne latent virus related)[1]	Allexivirus, type species for this genus[1]	S, o	None, or local chlorosis only		Mites (*Aceria tulipae*)	Probably same as shallot mite-borne latent virus SMbLV[1]; similar mite-borne virus in r[6]
IYSV[15]	Iris yellow spot virus	Tospovirus[1]	O, s, l, c, some wild alliums	Dry, straw-yellow lesions on leaves and scapes; seed stalk collapse	Up to 100% in seed crops; smaller bulbs[16,17]	*Thrips tabaci*, disease parallels thrips numbers[16,18]	Serious new disease in USA, Brazil, Israel and Spain

[a]All these genera except Tospovirus, which is spherical, are flexuous rods containing a single strand of RNA; relative lengths, Potyvirus > Alexivirus > Carlavirus[1].
[b]Crop species key: c, chive; cl, Chinese chives; g, garlic; ghg, great-headed garlic; j, Japanese bunching onion; l, leek; o, onion; r, rakkyo; s, shallot; w, Wakegi onion.
[c]Nt, nucleotide.
Other viruses reported in allium vegetables: TMV, tobacco mosaic in r[19]; TSWV, tomato spotted wilt virus in l, o[20]; TuMV, turnip mosaic virus in l[21]; several soil-borne viruses in s[10]; see also the list and references in Walkey (1990).
Data in table derived from the following sources: [1]ICTVdB Management (2006); [2]Schwartz and Mohan (2008); [3]Tsuneyoshi *et al.* (1997); [4]Lot *et al.* (1998); [5]van der Vlugt *et al.* (1999); [6]van Dijk and van der Vlugt (1994); [7]Chen *et al.* (2005); [8]Tsuneyoshi *et al.* (1998a); [9]Tsuneyoshi *et al.* (1998b); [10]van Dijk (1993); [11]Cafrune *et al.* (2006); [12]Sumi *et al.* (1999); [13]Song *et al.* (1998); [14]Chen *et al.* (2001); [15]Cortes *et al.* (1998); [16]Pozzer *et al.* (1999); [17]Gent *et al.* (2004); [18]Kritzman *et al.* (2001); [19]Chen *et al.* (1996); [20] Nischwitz *et al.* (2006); [21]Gera *et al.* (1997).



	1	2	3	4	5	6	7	8	9	10	11	12	
GV1	-	-	-	-	+	-	-	-	+	-	-	-	2/12
GV2	+	+	+	+	+	+	+	+	+	+	+	+	12/12
OYDV	-	+	+	-	-	+	+	-	-	-	-	-	4/12
mite-borne	-	-	-	-	-	-	-	-	+	-	-	-	1/12
symptomatic	-	+	+	-	+	+	+	+	+	+	-	-	8/12

Fig. 5.10. The molecular identification of viruses in 12 randomly selected garlic plants from a field in Aomori province, Japan. The photographs show bands on electrophoresis gels from Polymerase Chain Reaction (PCR) amplifications of DNA sequences characteristic of four different garlic viruses: GV1 carlavirus, GV2 potyvirus, OYDV onion yellow dwarf virus and mite-borne virus. The numbered columns show each of the 12 plants tested; columns N and P, respectively, are negative and positive controls for the diagnostic DNA bands, and column M gives a sequence of markers of increasing numbers of DNA base-pairs. The chart below the photographs indicates which viruses tested positive for each plant and, on the last line, which plants displayed visual symptoms of viral disease (from Takaichi *et al.*, 1998. Courtesy of *Plant Disease*).

traditional cultivars revealed some plants that had no or very mild symptoms of viral disease in field trials in several regions. Selection from such plants resulted in the development of virus-free named cultivars – for example, cv. 'Thermidrome' and some 'virus-tolerant' cvs (e.g. 'Fructidor' and tolerant strains of 'Violet de Cadours').

In the 1970s, techniques of eliminating viruses by 'meristem tip culture' were developed. Virus-free plants can be produced by culturing 0.5–0.8 mm-diameter explants of shoot apical meristem in tubes of sterile nutrient agar. Ultimately, rooted plantlets develop that can be transferred to soil (Walkey, 1990). Elimination of viruses from 'tolerant' strains of 'Violet de Cadours' increased yields by about one-third, and the virus-free cv. 'Germidor' was derived in this way. Meristem tip culture has been used to produce virus-free clones of numerous garlic cvs, resulting in larger bulbs with more cloves and 25–40% increases in bulb weight (see Fig. 5.11). Meristem tip culture was also used to develop virus-free shallot cvs 'Jermor' and 'Mikor', which have a yield potential of 40 t/ha, as opposed to a maximum of 25 t/ha in the previous best virus-tolerant strains (Messiaen *et al.*, 1993).

A system of multiplication, inspection, certification and distribution of virus-free garlic and shallots, the first in the world, was established in France in the 1960s (Messiaen *et al.*, 1993). This involves maintaining elite, disease-free clones of the named cvs in net houses to protect them from aphid virus vectors and multiplying the first two generations of bulbs for planting stock under these conditions. A further four generations of multiplication for garlic – or three for shallot – are carried out by selected growers in regions not conducive to the spread of viruses. Fields for propagation must be isolated by at least 300 m from other alliums. During growth, plants are inspected regularly for

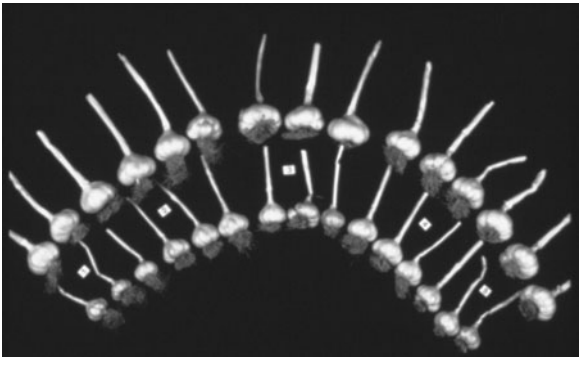


Fig. 5.11. Virus-free garlic bulbs (upper crescent) produced by meristem tip culture, compared with infected bulbs of the same cultivar (lower crescent). Three bulbs each of cvs (1) 'Rose de Var, (2) 'Printanor', (3) 'Blanc de la Drome', (4) 'Moulinin' and (5) 'Fructidor' after 1 year of growth in the field (× 1/9) (photograph courtesy of Dr D.G.A. Walkey, formerly of HRI Wellesbourne, UK).

signs of virus disease, as well as sampled, to ensure they are free of stem and bulb nematode and white rot. Any diseased plants found during inspection, plus adjacent plants, are removed and destroyed. A score of fewer than 1% of diseased plants in the final generation of multiplication is required for certification as 'virus-free' planting stock (Messiaen *et al.*, 1993).

Reinfection of virus-free garlic with OYDV or LYSV or a mixture of the two showed that OYDV caused more severe symptoms and yield loss than LYSV (Lot *et al.*, 1998). Yield loss, which was associated with earlier maturity of the infected plants, varied with cultivar, ranging 40–60% for OYDV, 17–54% for LYSV and 60–90% for the mixture. Similar experiments on reinfection with GarV-A and GarV-C showed smaller, but still significant, yield losses, being about 14–32% for GarV-A and 6–11% for GarV-C, again depending on cultivar (Cafrune *et al.*, 2006).

Given such immediate and large decreases in yield from artificial reinfection, the question arises whether the expense and effort of producing virus-free planting stock can be justified in some countries. Field trials in both Argentina and Brazil showed that yields from virus-free planting cloves, which were more than double those from the chronically infected local strains in the first year, declined exponentially with successive years of replanting. Despite this, after 7 years, yields from the originally virus-free stock remained significantly higher than from the local, chronically infected planting stock, indicating a continuing benefit over many seasons from planting virus-free material (see Fig. 5.12).

As observed in the above-mentioned French trials, healthy plants of both garlic and shallot not infected or not showing symptoms often occur among symptomatic plants (van Dijk, 1994). Also, there are reports of virus-tolerant garlic cvs that show no yield improvement after virus elimination by meristem tip culture (Walkey and Antill, 1987). These effects may be caused by infections with mild virus strains which 'cross-protect' their hosts and prevent infection

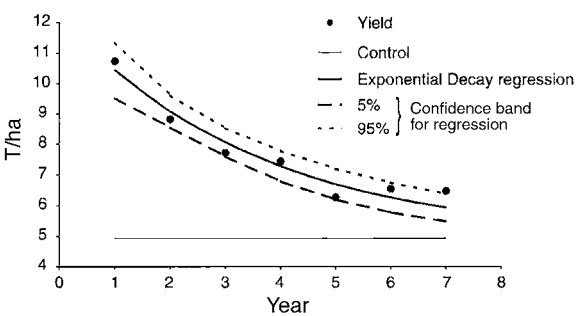


Fig. 5.12. Garlic yields from cloves that were virus-free in year 1 over 7 successive years of saving cloves and replanting in Brazilian trials. The 'control' line represents the yield from standard virus-infected cloves used by growers. The yields of virus-free stock showed an exponential decline with time (from Melo Filho *et al.*, 2006. Courtesy of the *European Journal of Plant Pathology*).

with virulent viruses (Walkey and Antill, 1987; van Dijk, 1994). Exploitation of such virus-tolerant planting material could improve yields in regions where the finance and infrastructure for the production of virus-free stock is not available (van Dijk, 1994). Another way of avoiding the problems of virus accumulation in vegetative planting stock is to grow from true seed. Seed-sown shallot cultivars are already available (Rabinowitch and Kamenetsky, 2002), and work is in progress to develop garlic cultivars grown from true seed (see Chapter 3).

As with nearly all crop protection problems, the situation with allium viruses is constantly evolving. In 1998 details of a newly recognized Tospovirus that causes yellow necrotic spots on the leaves of iris plants were reported from The Netherlands (Cortes *et al.*, 1998). In 1999 it was reported that a disease which had been causing severe yellowing and necrosis of onion leaves and scapes in Brazil since 1994, often resulting in the death of flowers and 100% losses of bulb and seed production, was caused by the same virus (Pozzer *et al.*, 1999). The same disease was reported from Israel and it was established the virus vector was the onion thrips, *Thrips tabaci* (Kritzman *et al.*, 2001).

The spread of this disease in onion-growing states of the western USA has been documented by a series of reports (e.g. Gent *et al.*, 2004b). In the USA the most severe losses have been in seed crops, where necrotic lesions have caused the collapse of seed stalks. However, losses in bulb crop yield – particularly of the valuable, larger size-grade bulbs – are of concern (Gent *et al.*, 2004b). The host range of the virus is narrow (Cortes *et al.*, 1998). Research on disease control has focused on avoiding disease carry-over in infected volunteer plants and on trying to control the thrips vectors of the virus. The disease can be particularly devastating in hot onion-growing regions like the Sao Francisco valley of north-eastern Brazil, probably because thrips proliferate very fast under the warm conditions. Observational evidence indicates there may be differences between onion cultivars in susceptibility to the disease, which may be linked with their attractiveness to thrips.

A virus-like disease of onions and leeks is caused by the phytoplasma aster yellows (Schwartz and Mohan, 2008; Bertaccini *et al.*, 1999). This can infect many vegetable species. In onion it produces flat, yellow-streaked leaves and distorted, sterile flowers. The disease is transmitted by a leaf hopper and can be controlled by insecticidal treatments against these vectors, the isolation of onions from other infected crops and the removal of weed hosts of the phytoplasma.

BACTERIAL DISEASES

Bacterial diseases of onion were reviewed in depth by Mark *et al.* (2002), and useful illustrations and information can be found in Snowdon (1991) and Schwartz and Mohan (2008). Bulb rots caused by bacteria are the most widely reported problem, but bacterial leaf blights can be devastating in some regions. Details of the main bacterial diseases are outlined in Table 5.4.

Table 5.4. Bacterial diseases of allium vegetables.

English name	Causal bacteria	Symptoms	Points of note
Sour skin or bacterial canker (see Plate 5b)	*Burkholderia cepacia* (formerly *Pseudomonas cepacia*)	Macerated, sour-smelling, mushy bulb scales; grainy yellow ooze under infected scales; spreads within, rather than between, scales; on leaves, lesions and leaf death	Checked by drying out of infected leaves and bulb necks; can persist in soil
Bacterial streak or bulb rot	*Pseudomonas viridiflava* (similar to *P. syringae*)	Dark, water-soaked streaks on leaves spreading to leaf base and into bulb; causing total foliar collapse in severe cases; milder infections causing pale yellow turning to red-brown rotten centre bulb scales after harvest	Survives as surface dweller (epiphyte) on many weeds; very destructive to N-rich succulent onions
Centre rot	*Pantoea ananatis* (closely related to *Erwinia herbicola* – synonym *Pantoea agglomerans*)	Water-soaked, white-bleached centre leaves surrounded by brown tissue; macerated, foul-smelling bulb interior; also infects seed stalks	Pathogenic on several other crops including pineapple; epiphytic on many weeds; transmitted by thrips and seed-borne[1]
Bacterial soft rot (see Plate 5a)	*Erwinia* sp. of the 'carotovora' group, including *E. carotovora* ssp. *carotovora*, *E. chrysanthemi*, *E. herbicola*, *E. rhapontica*	Soft yellow to brown rot starting in bulb centre releasing foetid-smelling, viscous, watery fluid	Short-lived in soil but persists in rhizosphere; survives in intestine of onion fly larvae and adults; infects most vegetable alliums
Slippery skin or other soft rots (see Plate 5c)	*Burkholderia gladioli* pv. *alliicola* (formerly *Pseudomonas alliicola* or *P. gladioli* pv. *alliicola*), *P. aeruginosa*, *P. marginalis*, *Lactobacillus*, *Enterobacter cloacae*	Rotten inner scales spreading to the whole bulb; the infected core can slip out of the top of the onion bulb when squeezed, hence the name 'slippery skin'; some species also infect green leaves	*B. gladioli* pv. *alliicola* infects via wet neck wounds when onions topped at harvest; bulb rot promoted by high-temperature drying (*c.* 30°C); can be spread by planting infected sets[2]

Onion leaf blight	*Xanthomonas axonopodis* pv. *allii* (formerly *X. campestris*)[3,4]	Lenticular, water-soaked leaf spots that elongate into chlorotic streaks leading to leaf death; devastating to yield when foliage collapses at the start of bulbing	Seed-borne[6]; epiphytic on many weeds and other crops; spreads in infected irrigation water; epidemics when wet, windy weather is followed by high temperatures[5,6]
Leek leaf necrosis	*Pseudomonas syringae* pv. *porri* a virulent disease-causing variant of *P. syringae*, a widespread species found on many host plants[7]	Water-soaked leaf lesions with a yellow halo that coalesce into light brown streaks; leaf tips die and leaves fold like a shepherd's crook; similar sunken lesions on flower stalks[8]	Probably seed-borne[8] as most strains are genetically very similar worldwide; raising seedlings at high densities in humid greenhouses, followed by leaf trimming at planting then sprinkler irrigation favours infection[9]

Based primarily on information from Mark *et al.* (2002) with additional points from the following references superscripted in the table: [1]Gitaitis *et al.* (2003); [2]Davies and Taylor (1994); [3]Gent *et al.* (2004); [4]Roumagnac *et al.* (2004a); [5]Schwartz *et al.* (2003); [6]Roumagnac *et al.* (2004b); [7]Samson *et al.* (1998); [8]Noble *et al.* (2006); [9]Koike (1999).

General characteristics of bacterial diseases

Symptoms and infection

Pathogenic bacteria cause infected tissue to become macerated and water-congested through the destruction of plant cell walls by their pectolytic enzymes. Extracellular polysaccharides embed the bacteria and are thought to induce water-congested intracellular spaces within which the bacteria can spread. In onion bulbs, bacterial infection often spreads within, rather than between, fleshy scales.

Moisture is necessary for initial infection, and ingress is often via wounds. Bacterial diseases of onion are favoured by warm temperatures, frequently with optima around 30–32°C. Wet, windy weather followed by warm temperatures is conducive to disease. Wind will cause leaf damage, rain-splash facilitates the spread and entry of bacteria and warmth accelerates subsequent rapid disease development. Potential causes of damage include leaves snapping under their own weight and by wind movement, abrasion by hail and wind-blown soil particles, cultivation operations, trimming to remove foliage from onion necks at harvest or before transplanting seedlings and damage by pests.

Both soil particles and cultivation equipment can be contaminated by pathogenic bacteria. Equipment can brush past and pick up the bacteria from weeds or other crops on which they may exist as asymptomatic surface colonizers (epiphytes). Some of the pathogenic bacteria have been shown to survive within the digestive tracts of pests – for example, *Erwinia carotovora* spp. *carotovora* within larvae and adults of the onion fly, *Delia antiqua* and *Pantoea ananatis* can survive within, and infect onions via, the tobacco thrips, *Frankliniella fusca* (Gitaitis *et al.*, 2003). When onion leaves fold under their own weight the inner side of the fold can retain moisture and present a vulnerable point of ingress for leaf blight bacteria (Gitaitis *et al.*, 1997). In wet weather water can accumulate where young leaves emerge from the top of the pseudostem, and this region has been shown to be very susceptible to infection by *Burkholderia cepacia*. Onion bulbs are susceptible to infection around harvest time when bulb rot bacteria can invade leaf tissue and enter the top of the bulbs via the neck if leaves and cut necks are wet (Wright and Triggs, 2005).

Diagnosis

The identification of the primary pathogen causing a bacterial rot is not always straightforward, since rotting tissue can be invaded by numerous secondary opportunistic microorganisms when it starts to decay. The aggressive pathogen must be distinguished from these and identified. In novel situations, the suspected pathogen isolate must be shown to induce disease in healthy plants when they are inoculated with it. The identification of bacterial pathogens is technically demanding and frequently involves 'polyphasic characterization', where a range of different biochemical, DNA-based and sometimes immunological methods are combined to establish identity (e.g. Gent *et al.*, 2004a; Roumagnac *et al.*, 2004a). Sometimes, rapid and sure diagnostics can be designed, increasingly using PCR-

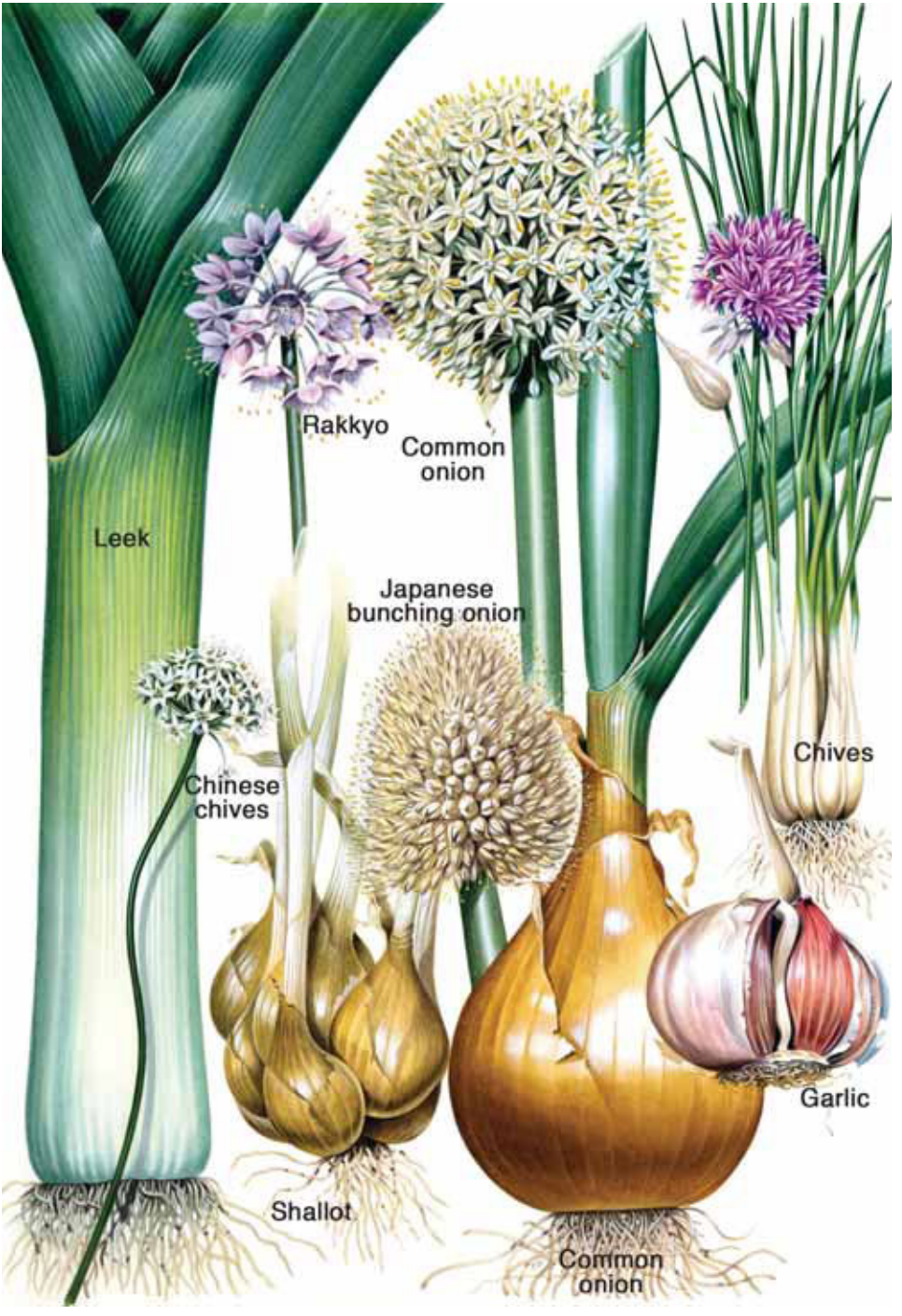


Plate 1. Shoots, bulbs and inflorescences of important vegetable alliums. The linear dimensions are approximately 60% natural size (from an original illustration by John Pendleton of Design Principles, Kineton, Warwick, UK©).

Plate 2. An illustration emphasizing the characteristic symptoms of a number of the important diseases of onions in temperate regions (from a poster by Sue Wickison, published by the Vegetable Research Trust, Wellesbourne, UK©).

3a

3b

3c

Plate 3. Pest damage on onions. (a) Thrips, *Thrips tabaci*, damage where leaf blades emerge from the neck of an onion plant, showing the silvering of the leaf as a result of thrips puncturing cells and feeding on the contents (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©). (b) Damage to young onions caused by subsoil feeding along the plant row by onion fly larvae, *Delia antiqua* (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©). (c) Onion fly, *Delia antiqua*, damage to an onion bulb. A whitish larva can be seen emerging near the base of the bulb (image kindly provided by Warwick HRI, Wellesbourne, UK©).

4a

4b

4c

Plate 4. Pest damage on onions. (a) Leaf miner, *Lyriomyza* spp., damage on onion (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©). (b) Damage, frass and larva of leek moth, *Acrolepiopsis assectella* (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©). (c) Characteristic distorted growth of onion caused by stem and bulb eelworm, *Ditylenchus dipsaci* (image kindly provided by Warwick HRI, Wellesbourne, UK©).

5a

5b

5c

Plate 5. Bacterial disease symptoms on onions. (a) Leaf collapse in the field caused by leaf base rotting from infection with *Erwinia carotovora*, bacterial soft rot (image kindly provided by Bejo Zaden B.V., Warmenhuizen, The Netherlands©). (b) Bulbs with a vinegar-smelling rot caused by sour skin infection, *Burkholderia cepacia* (formerly *Pseudomonas cepacia*) (image kindly provided by Bejo Zaden B.V., Warmenhuizen, The Netherlands©). (c) The early-stage symptoms of slippery skin infection, *Burkholderia gladioli* p.v. *allicola* (formerly *Pseudomonas gladioli* p.v. *allicola*) (image kindly provided by Bejo Zaden B.V., Warmenhuizen, The Netherlands©).

6a

6b

6c

Plate 6. Fungal leaf disease symptoms. (a) Lesion on onion leaf caused by purple spot infection, *Alternaria porri* (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©). (b) White flecking and leaf lesions on onion caused by leaf blight, *Botrytis squamosa* (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©). (c) A 'fur' of sporing bodies forming on an onion leaf infected with downy mildew, *Peronospora destructor* (image kindly provided by Bejo Zaden B.V., Warmenhuizen, The Netherlands©).

7a

7b

7c

Plate 7. Fungal leaf disease symptoms. (a) Onion leaves collapsing from the tip as a result of white tip infection, *Phytophthera porri* (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©). (b) Leek leaf showing leaf yellowing and orange-brown sporing eruptions from leek rust infection, *Puccinia allii* (image kindly provided by Warwick HRI, Wellesbourne, UK©). (c) Young leaves and shoot bases with black, blister-like lesions from onion smut infection, *Urocystis cepulae* (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©).

8a

8b

8c

Plate 8. Soil-borne disease infection of roots and stem bases. (a) White rot, *Sclerotium cepivorum*, attack on stem bases of salad onions showing white mycelial masses and patches of black sclerotia (image kindly provided by Warwick HRI, Wellesbourne, UK©). (b) Pink root, *Pyrenochaeta terrestris*, symptoms on onion (image kindly provided by Bejo Zaden B.V., Warmenhuizen, The Netherlands©). (c) Onion stem bases infected by Fusarium basal rot, *Fusarium oxysporum* f.sp. *cepae* (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©).

9a

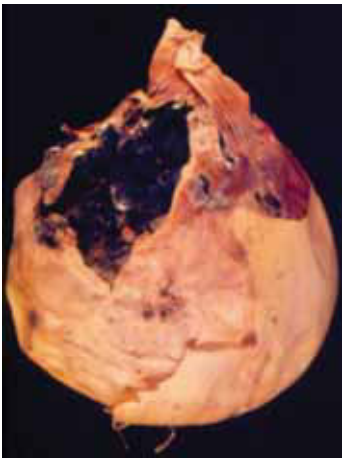


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Plate 9. Fungal disease symptoms on onion bulbs. (a) Black scleroial masses on the outside of a bulb infected by *Botrytis allii* (image kindly provided by Warwick HRI, Wellesbourne, UK©). (b) Internal rot caused by neck rot, *Botrytis allii*, infection on onion bulbs (image kindly provided by Bejo Zaden B.V., Warmenhuizen, The Netherlands©). (c) Black mould on outer fleshy scales of bulb caused by *Aspergillus niger* (image kindly provided by Bejo Zaden B.V., Warmenhuizen, The Netherlands©). (d) Onion smudge, *Colletotrichum circinans*, on outer scales of onion showing black dots of stromata, some in characteristic concentric circular rings (image kindly provided by De Groot en Slot B.V., Broek op Langedijk, The Netherlands©).

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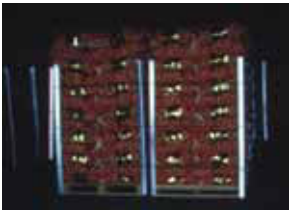

Plate 10. Onion storage, grading and packing. (a) Modern bulk onion store with onions in bulk bins and stored directly on the floor to a depth of 5 m. (b) Overview of cleaning, grading and quality control operations after removal from store. (c) Automatic size grading machine. (d) Automatic filling and weighing of nets containing 25 kg of onions. (e) Conveying filled nets. (f) Automatic stacking of nets on to a pallet. (g) Filled pallets ready for dispatch to supermarket depot or wholesaler.

based methods, and these can facilitate research on pathogen biology, e.g. for detection of the pathogen in soil, on seeds or as an epiphyte on weeds and other crop species.

The techniques used to identify bacteria include:

1. Examining their appearance, including size, shape, colour of pigments produced, motility and flagellae.
2. Identifying the substrates on which they can grow. Commercially available microplate systems are available to detect which of a large array of carbohydrates a bacterium can assimilate.
3. Other biochemical and physiological traits are used, including: (i) characteristic exudates; (ii) the capacity for nitrate reduction; (iii) the acidification of a glucose medium; (iv) whether the bacterium can grow aerobically and/or anaerobically; and (v) the optimum temperature and pH for metabolic activities.

The resulting 'metabolic fingerprint' from the biochemical tests of (**2**) and (**3**) serves to identify the species.
4. The fatty acids of bacteria, which can be determined by gas-liquid chromatography, are used in their identification. They can be characterized both by the presence of particular fatty acids and the ratios of different fatty acids to each other.
5. The DNA sequence of the genes coding for ribosomal RNA (rRNA) are species specific and can be determined by DNA sequencing (e.g. Roumagnac *et al.*, 2004a). From such information oligonucleotide primers for initiating PCR (polymerase chain reaction) amplification of rRNA genes have been designed. PCR amplification of DNA extracts from bacteria using such specific primers can be used rapidly and accurately to identify bacterial species (Mark *et al.*, 2002).
6. The DNA sequence of the spacer region between the 16S and 23S regions of the genes coding for ribosomal RNA is more variable than the sequences coding for the 16S and 23S regions themselves. Differences in this labile region, which can be picked up as differences of length or sequence, can be useful for identifying between different strains of a bacterial species.
7. As with higher plants, differences in fragment lengths following treatment of extracted DNA with different endonuclease enzymes (AFLP) can be used to identify bacteria (e.g. Roumagnac *et al.*, 2004a).

Epidemiology

Some details of how the various bacterial diseases persist and spread are given in Table 5.4. Infected crop debris is an important source of infection for most of these diseases. Bacteria generally persist longer on surface debris than on that which is ploughed under the soil. For example, the number of culture-forming units of *Xanthomonas axonopodis* pv. *allii* on onion leaves decreased 10^4–10^6 times after 9 months of burial 25 cm deep in soil compared to being left on the soil surface (Gent *et al.*, 2005). Infected volunteers of the allium crops are another potential source of inoculum.

Many bacterial pathogens can persist on the surface of other crops and on weeds. For example, *Xanthomonas axonopodis* pv. *allii* can survive epiphytically on dry bean crops in Colorado, USA and on a number of weeds common there. Survival on such vegetation does not normally persist for more than 1 year after a diseased onion crop has been grown (Gent *et al.*, 2005). In Georgia, USA, *Pantoea ananatis* and *Pseudomonas viridiflava* persist on a number of weeds of onion fields. *Pseudomonas viridiflava* was found on the cutleaf evening primrose several kilometres from onion crops and several years after onions had been grown nearby. An association was noticed between the herbicidal control of this weed in onion fields and the extent of crop infection (Gitaitis *et al.*, 1998).

Pseudomonas viridiflava was not found in soil or water in Georgia. On the other hand, *Burkholderia cepacia* can survive in soil for long periods, although its frequency increases with onion cropping (Yohalem and Lorbeer, 1997). Irrigation water that has drained off infected crops is another potential source of inoculum, as was shown for *X. axonopodis* pv. *allii* (Gent *et al.*, 2005).

A number of bacterial pathogens have been shown to be seed transmitted, as indicated in Table 5.5. The genetic similarity of most strains of *Pseudomonas syringae* pv. *porri* causing leek leaf blight around the world points to its transmission on seed from Europe, from where most leek seed is supplied (Noble *et al.*, 2006). Roumagnac *et al.* (2000) detected *X. axonopodis* pv. *allii* on a number of onion seed-lots. A study of disease development in fields sown with 0.04% infected seed showed a pattern of spread around random diseased plant foci, probably derived from infected seed, when warm weather followed wet, windy weather (Roumagnac *et al.*, 2004b). Infected onion sets can also originate disease. In the UK, onion bulb crops grown from sets were found to be infected with *Burkholderia gladioli* pv. *alliicola*, whereas crops grown from seed were not (Davies and Taylor, 1994).

The spread of bacterial disease depends on weather conditions, wetness being necessary for infection, with temperatures around 30°C being generally optimal for disease development. Schwartz *et al.* (2003) derived regression models relating the development of leaf blights to weather conditions in Colorado. For both *Pantoea ananatis* and *X. axonopodis* pv. *allii* blights, disease appearance was associated with high July temperatures and, for the latter disease, there was a strong association of severity with high temperatures in July and high rainfall in July and August.

Changes in agronomic practices often give rise to new disease problems. For example, bacterial rots of stored onions became prominent in the UK when forced ventilation drying using air around 30°C was applied to field-topped bulbs (Davies and Taylor, 1994). High temperatures were introduced to develop brown-coloured bulb skins (see Chapter 7), an attractive feature for purchasers.

Control measures

As always in plant pathology, rational control measures require knowledge of what is causing the disease and information on the life cycle of the pathogen,

including alternative host plants, survival in soil and in crop debris, modes of pathogen spread and how this is affected by weather. Disease management utilizes such information to avoid or minimize initial bacterial disease inoculum and to apply bactericides starting only when weather conditions make the spread of disease likely, thereby minimizing the risk of bactericide-tolerant strains of pathogen evolving.

Integrated disease management programmes to achieve these objectives must include:

1. Ensuring seed and sets are pathogen free. This is particularly important in the era of global seed companies trading seeds between countries and continents.
2. Maintaining good crop hygiene by removing or burying diseased debris, volunteer alliums and weeds on which the pathogens survive as epiphytes.
3. Utilizing crop rotations of non-host crops with a minimum of 1 year between allium crops. For example, small grain crops are recommended in rotations to reduce *X. axonopodis* pv. *allii*.
4. Separating vulnerable crops both in time and space so that there is not a continuous 'infection cycle' from one allium crop to another.
5. Avoiding excessive nitrogen fertilizer, which can result in luxuriant foliage that is easily damaged by wind and cultivation traffic and which tends to maintain a wet microclimate in the crop.
6. Minimizing damage to plants from cultivations and by having good pest control.

Conditions around harvest time can be critical in determining the level of bulb rot in stored onions. A series of studies near Pukekoe in New Zealand has shown that dry neck and leaf tissue is less prone to infection. The bacteria can invade the neck and enter the bulb by infecting the green leaves or through moist cut necks. The aim of harvesting systems should be to dry the onion necks and foliage as quickly as possible, to cut the foliage from the necks when they are as dry as possible and to ensure the necks dry quickly after cutting. Forced ventilation with dry air can help to achieve this. It is important to avoid wounding the tops of bulbs by cutting necks too low. Cutting without bulb damage is easier the drier the necks (Wright and Triggs, 2005). Bacterial bulb rots in store tend to be more serious following a wet harvesting season.

Resistant cultivars would be useful in disease control, but there are few reports of resistance to bacterial disease. Wright and Grant (1998) surveyed a wide range of allium species for resistance to leaf rot by strains of *Ps. viridiflava* and *Ps. marginalis* isolated from rotten onion bulbs. There were wide differences in susceptibility but most vegetable species included susceptible types, although there were highly resistant garlic and chive lines, as well as some resistant wild alliums. Different authors have reported differences in the susceptibility of other allium vegetables to *Ps. syringae* pv. *porri* virulent on leeks (Noble *et al.*, 2006). This may be because of differences in techniques or it may reflect genuine

variations in virulence of different strains of the pathogen. In a study of tropical onion cultivars, those with a high dry matter percentage and small bulbs were most resistant to bacterial bulb rots (Swee-Suak Ko *et al.*, 2002).

Bactericides are used to prevent disease outbreaks and slow or prevent epidemics, particularly of leaf blights. The most widely used bactericides are copper-based, but zinc and some other metallic ions are bactericidal. Some contain copper hydroxide, others chelated copper. Copper-based formulations are preventative, while surface-acting bactericides and sprays need to be initiated before infection enters the plant. There are reports of pathogens being resistant to copper fungicides, and bactericides combining copper and maneb (an ethylene bisdithioocarbamate (EBDC) fungicide) are currently the most effective control strategy. In Colorado, applications every 5–10 days of this combination as a high-volume spray to ensure complete leaf coverage is recommended for the control of *X. axonopodis* pv. *allii*, starting 2 weeks before bulb initiation. This results in eight or more sprays per crop. EBDC fungicides are carcinogenic, and there is regulatory pressure to reduce and even cancel their use in future (Gent and Schwartz, 2005).

Four sprays of acibenzolar-S-methyl – a chemical elicitor of plant systemic acquired resistance (SAR) to pathogenic infections in general (Vallad and Goodman, 2004) – were as effective in control of *X. axonopodis* pv. *allii* leaf blight as nine to 12 sprays of copper plus maneb (Gent and Schwartz, 2005). However, there is a 'metabolic cost' to the plant in activating its systematic defences and, in the absence of disease, the yield of acibenzolar-S-methyl-treated onions was about 24% lower than an untreated crop. Sprays of the competitive bacteria *Pantoea aglomerans* and *Pseudomoas fluorescens* also reduced infection, and biological control by bacterial antagonists may provide another alternative to conventional bactericides in future (Gent and Schwartz, 2005).

FUNGAL LEAF DISEASES

There are a number of diseases caused by fungal pathogens that destroy the leaves of edible alliums. These diseases were reviewed in detail by Maude (1990a) and Schwartz and Mohan (2008). Additional information on some diseases can be found in Sherf and Macnab (1986), Snowdon (1991) and Maude (2006). Destruction of foliage leads to low yields of bulbs with shortened storage potential. Leaf disease lesions on alliums harvested as leafy crops – for example, salad onions – can lead to their rejection and a complete loss of crop. Therefore, it is important to prevent these diseases. Leaf diseases divide roughly into two categories, those prevalent in temperate regions and those of warmer subtropical and tropical areas (Maude, 2006). The temperature ranges and optima for pathogenesis and disease development reflect this division. Table 5.5 lists and summarizes some of the basic information regarding these diseases. It

is apparent from Table 5.5 that the different diseases have many common features in their life cycles and in measures for their control.

A sequence of events occurs in the development of disease. First, there must be a primary source of infection from which spores of the pathogen arrive on the crop leaves. If environmental conditions are conducive, spores can germinate, penetrate and infect leaves. There follows the 'latent period' during which infection spreads within the leaf. At the end of the latent period the pathogen has the capacity to sporulate when environmental conditions are suitable. When the infected leaf produces spores, a second cycle of infection and disease is initiated. Depending very much on weather conditions, as well as on the influence of protectant fungicides that may have been applied, and possibly on antagonism from other leaf surface fungi, the spores from the first cycle may infect a larger leaf area and progress towards an epidemic. Total leaf devastation in three or four cycles can occur in weather conditions conducive to disease spread. Alternatively, the disease may peter out if the infected leaf area in the second cycle is less than the first and continues to decline with each cycle.

Most leaf-infecting fungal pathogens require periods of high humidity along with temperatures within a certain range to sporulate. They often require darkness for sporulation and hence spores form at night. Spore release is frequently triggered by light and a decrease in humidity the following morning. The quantity of spores formed can increase the higher the humidity and peak around a temperature optimum (see Fig. 5.13). Once released the spores have a limited life – for example, downy mildew conidia remain viable for just 3 days (Jesperson and Sutton, 1987). Once they have landed on a leaf, the spores typically require a minimum duration of leaf wetness – along with temperatures within a specific range – to germinate and penetrate the leaf and infect it. The duration of leaf wetness needed may be shorter at optimal temperatures for infection (see Fig. 5.14).

The latent period tends to be shorter the warmer the temperature, provided it remains within the range tolerated by the pathogen. The duration of the latent period is also shortened by increased density of infecting spores, possibly because this causes rapid depletion of resources available to the pathogen which, in turn, triggers sporulation. For example, for leek rust the latent period is shortest at 19–22°C and decreases by about 1.8 days for every tenfold increase in spore density (Gilles and Kennedy, 2003). Similar trends were found for onion downy mildew (Hildebrand and Sutton, 1984).

For all these diseases, debris from previous infected crops left on the soil surface or in waste heaps can act as a primary source of infection for the next crop. During the growing season spores produced on nearby infected crops can also introduce infection to a field. Where successive crops overlap in time, for example with over-wintered and spring-sown onion crops in temperate regions like maritime western Europe, infection can 'bridge' from a crop to the following crop, resulting in an uninterrupted series of disease cycles.

Table 5.5. The fungal foliar diseases of vegetable alliums: their symptoms, epidemiology and control.

Disease and pathogen[a]	Host crops[c] and distribution[d]	Symptoms	Infection sources	Conditions for spore production	Conditions for infection	Fungicides	Resistance	Cultural control	Special features
Purple blotch[b], *Alternaria porri* (see Plate 6A)	O, g, j, l Tr, st	2–3mm watery lesions on leaves and flower stalks which elongate and bleach, with purple/brown centres, rot of infected bulbs	Debris, infected bulbs	Light, RH > 90%, spore release with RH drop, 25°C optimal, little at < 13°C	25°C, free water on leaf for 6 h, older and damaged leaves more susceptible (e.g. by thrips)	Dithiocarbamates, iprodione, mancozeb, chlorothalonil, vinclozolin, vary fungicides to avoid resistant pathogens	Cv. differences	Long rotation, hygiene, minimize leaf wetness by wide spacing, moderate N, high P and K	Often in disease complex with *Stemphylium vesicorum* [1,2,3], saprophyte fungus *Aureobasidium pullulans* on leaves lessens infection
Leaf fleck, leaf spot, collar rot, *Botrytis cinerea* (see Plate 2)	O, wide host range Te	Small leaf spots, rot round pseudostem with grey mould on it	Debris, nearby crops, sclerotia in soil	Can occur at low temp. (5°C)	Plants stressed by cold (collar rot)	As for *B. squamosa*		Avoid crop overlap, hygiene	Worsened by ozone damage
Leaf blight[b], blast, *Botrytis squamosa* (see Plates 2 & 6B)	O Te	Small, round to ellipsoid white lesions with pale halo, leaf die-back from tip, sporing on dead leaves	Sclerotia in debris and soil which form conidia (spores), nearby crops	14–20°C, free water for > 12 h, spore release with RH change	6–28°C, free water on leaf for > 6 h, old and senescent leaves susceptible	Dithiocarbamates, benzimidazoles	J, c, *A. roylei* from which resistance is being transferred to onion	Avoid crop overlap, hygiene, promote air movement and leaf drying by wide spacing, rotation	Forecasting models made, worsened by ozone damage, resistance to benzimidazole fungicides reported
Leaf spot, *Cercospora duddiae*	O, g, s and many allium hosts St, tr	Leaf spots with red edges, brown spore masses	Debris, volunteers, wild alliums	Warm and wet	Warm and wet	Protectant fungicides routinely applied – captan, maneb, Bordeaux mixture, thiobendazole		Rotation, remove allium weeds	

Leaf blotch, *Cladosporium allii-cepae* on onion and others, *C. allii* on leeks (see Plate 2)	O, s, l, gh, j and other alliums L, gh (*C. allii*) Te	Elliptical white blotch, total foliage bleaching, olive/brown sporing patches	Nearby crops, debris	2–20°C, optimum 5.0–8.5°C after 8 h dark, RH > 90%, low light	>17 h at 100% RH, 15–20°C optimal, old and senescent leaves and leaf tips	Iprodione, maneb and chlorothalonil or fentin acetate every 14 days late in season	Unlikely	Avoid crop overlap, prevent spore spread at harvest, rotation > 2–3years	Usually occurs after bulbing starts, also on overwintering crops in UK
Twister, seven curls, anthracnose, *Glomerella cingulata*	O and many hosts St, tr	Twisted, curled leaves, chlorosis, long necks, white lesions, pink spores	Debris, alternate hosts, seeds		23–30°C, high RH, rain-splash and wind-spread infection	Zineb, ferbam, captan, dithane or copper formulations		Hygiene	Insects and irrigation water can spread spores
Powdery mildew, *Leveillula taurica*	O, g, l[4] Te, st	5–15 mm yellow, circular lesions on leaves forming powdery conidia		Infects via stomata, particularly on older leaves					Rare, infects cvs lacking leaf wax[5]
Downy mildew[b], *Peronospora destructor* (see Plates 2 and 6C)	O, s, g, j, c Te	Pale, elongated patches on leaves forming grey/purple felt of sporing bodies, chlorosis and collapse of leaves and flower stalks	Debris, crop overlap, volunteers, systemically infected bulbs or sets	3–25°C, 100% RH, spores form at night and release with RH drop in day, 9–16 days latent period between infection and spore production	Optimum 10–12°C, free water on leaf for 2–4 h	Dithiocarbamates, copper, chlorothalonil. Fosetyl-Al, metalaxyl, alternate different fungicides to avoid pathogen resistance	Cv. differences reported, resistance from *A. roylei* being transferred to onion (see Chapter 3)	Avoid crop overlap, hygiene, rotation > 4 years; to minimize RH round leaves, use wide spacing, orient rows parallel to prevailing wind and use moderate N	Heat-treat infected bulbs for 4 h at 41°C, forecasting models developed

continued

Table 5.5. *continued*

Disease and pathogen[a]	Host crops and distribution	Symptoms	Infection sources	Conditions for spore production	Conditions for infection	Fungicides	Resistance	Cultural control	Special features
White tip of leek[b], *Phytophthora porri* (see Plate 7A)	O, g, l, r Te	White lesions 3 × 5 cm, particularly at leaf tips, bulb rot of o and r	Soil-, rain-splashed oospores[6], infected leaves		Leaf contact with water associated with rain, 120 DD (>3°C) from infection to lesions[6]	Chlorothalonyl and metalaxyl, mancozeb and metalaxyl	Resistance genes in some cvs and landraces	> 3 year rotations	Serious in overwintered crops, oospores survive > 5 months in soil
Onion rust, leek rust[b], *Puccinia allii*, different strains for onion and leek (see Plates 2 and 7B)	O, s, g, j, l, gh, c Te, st, tr	White flecks with orange pustules of uredospores, 1–3 mm long	Nearby crops, debris		10–24°C, > 4 h at RH > 97%	Maneb, zineb, fenpropimorph (for leeks)	Partial in some l cvs, improved by selection in j[7]	Avoid crop overlap, hygiene, 4–5 year rotation	Worse on stressed plants, disfiguring on crops harvested leafy
Black (stalk) mould, *Stemphylium botryosum*, sexual stage forming ascospores, *Pleospora herbarum*	O, l and many hosts Te, st	Spots, then browning and black mould, collapse of leaf or seed stalk	Debris, possibly infected seed	Cool, moist conditions	Attack by other pathogens, e.g. *Botrytis* or mildew	As for downy mildew or *Botrytis*	Cv. differences	Hygiene, avoid crop damage which creates necrotic tissue	Often secondary, invading tissue damaged by downy mildew or *Botrytis*

Stemphylium leaf blight and stalk *rot, Stemphylium vesicarium,* ascospore-forming stage is *Pleospora allii*	O, g, l Te, st	Small, white to brown watery leaf spots elongating to spindle-shaped patches with dark brown or black centres where conidia form	Ascospores from infected debris in late winter[8], conidia from debris in spring and from infected plants as epidemic develops[8]	10–21°C, > 14 h at < 5 mb VPD for ascospores[8], rainfall and 15–32°C for conidia	> 8 h leaf wetness at 10–25°C, more infection with longer wetness[1] and higher temp. (up to 20°C), tissue damage by other pathogens	As for purple blotch	As for purple blotch	Symptoms difficult to distinguish from *Alternaria porri*[1,2,3], often occurs with the latter as a disease complex, causes collapse of flower stalks
Smut, *Urocystis cepulae or U. colchici* (see Plates 2 and 7C)	O, s, l, j, c Te	Thickened areas several mm long on young leaves, forming black, powdery spore masses, twisted leaves	Spores in soil, infected sets or transplants	Infected as cotyledon or young leaves penetrate soil, 13–22°C optimum, inhibited at > 29°C		Seed treatment with thiram, captan, ferbam or folpet	Plant sets or seedlings as these cannot be infected, sow when temperatures favour rapid seedling emergence (less time for infection)	Infects cotyledons and young leaves as they penetrate soil, hence infection period is short, spores can live > 25 years in soil

C, chives; g, garlic; gh, great-headed garlic; j, Japanese bunching onion; l, leek; o, onion; r, rakkyo; s, shallot; te, temperate; st, subtropical; tr, tropical.

[a] Ordered alphabetically by pathogen name.

[b] The more important diseases and pathogens.

Main sources: Schwartz and Mohan (2008), Maude (1990a, 2006), Snowdon (1991) and Sherf and MacNáb (1986); additional references indicated as superscript numbers in the table: [1]Suheri and Price (2000a); [2]Suheri and Price (2000b); [3]Suheri and Price (2000c); [4]Kurt *et al.* (2004); [5]Mohan and Molenaar (2005); [6]Smilde *et al*, (1996); [7]Yamashita *et al.* (2005); [8]Prados-Ligero *et al.* (2003).

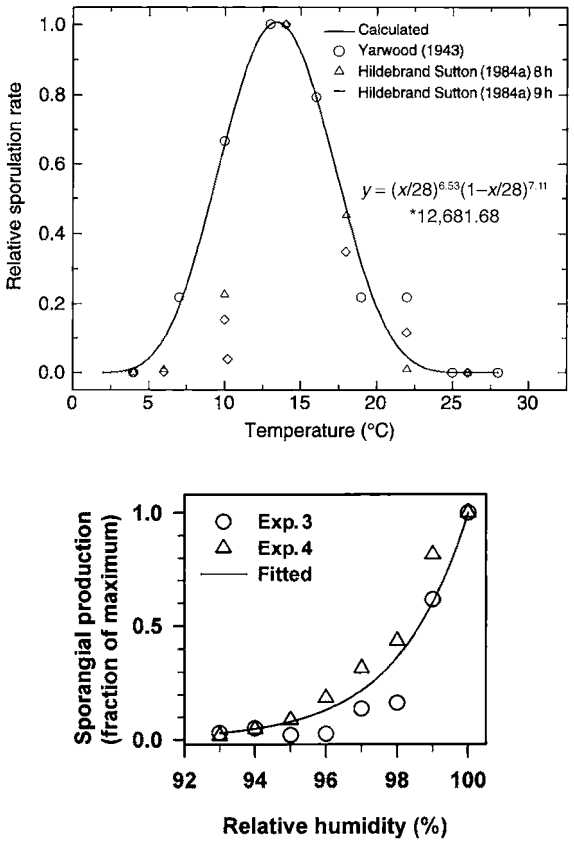

Fig. 5.13. Microclimate effects on the development of sporangia by onion downy mildew, *Peronospora destructor*. (a) The effect of temperature on relative sporulation rate, derived by combining data from the authors listed in the graph (from Friedrich *et al.*, 2003. Courtesy of the *European Journal of Plant Pathology*). (b) The effect of relative humidities (range 93–100%) on the relative number of sporangia produced on onion leaves in two separate experiments (○ and △) after 14 h at 12°C in darkness (from Gilles *et al.*, 2004. Courtesy of *Plant Disease*).

The means by which leaf pathogens survive and spread in the absence of growing crops vary, and detailed knowledge of the biology of each pathogen is needed. Several can survive as long-lived, dormant structures in the soil – for example, onion smut chlamydospores, leek white tip oospores and the sclerotia of *Botrytis* leaf blights (see Table 5.5). Knowledge of the conditions for survival and germination of these dormant stages is important for disease management. For example, *Botrytis squamosa* forms dark-coloured, irregular, roughly ellipsoidal sclerotia 3–10 mm long on decaying onion waste. In a study on organic soil in

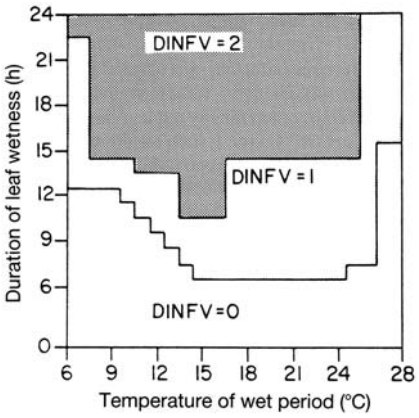

Fig. 5.14. Chart for determining the daily infection values (DINFV) in the BOTCAST model for forecasting the progress of leaf blight caused by *Botrytis squamosa* on onions from temperatures and durations of periods of leaf wetness. DINFV = 0, not conducive to infection; DINFV = 1, conducive to light infection; DINFV = 2, conducive to severe infection (from Sutton *et al.*, 1986. Courtesy of *Agriculture, Ecosystems and Environment*).

New York State, these showed 66% survival after burial 15 cm deep for 21 months (Ellerbrock and Lorbeer, 1977). After germinating, sclerotia give rise to conidia, or sometimes ascospores, which disperse and infect leaves. Sclerotia germinate between 5 and 25°C, fastest at 16°C, but produce the most conidia at 10°C. Germination rate and the number of conidia produced decline as soil water potential decreases, although 60% sclerotial germination occurs in water potentials as low as –2MPa (Clarkson *et al.*, 2000). Other pathogens perennate in infected volunteer plants or bulbs, e.g. downy mildew, where infected onion sets and mother bulbs for seed crops act as primary disease sources.

Disease control

Rational disease control rests on a detailed knowledge of the biology of the pathogen and its interaction with the host crop. The life cycle of the pathogen must be known, including how it perennates and spreads, so that primary sources of infection can be identified and, if possible, eliminated. Knowledge of the weather conditions favouring sporulation, infection and disease development enables potential epidemics to be predicted, and preventive measures to be taken.

Crop hygiene is universally important in disease control. Potentially infective crop residues and waste must be identified and destroyed. It is important to avoid the spread of diseased debris on farm vehicles and equipment and on the boots of workers. Volunteer plants appearing after a crop has

been cleared, or on tracks and waste land, are potential sources of disease persistence and should be destroyed, as should any alternative hosts like susceptible weeds. After harvest, crop remains normally break down much faster and have less time and opportunity to form spores if they are buried than if they are left on the soil surface.

For example, *Stemphylium vesicarium* can cause severe leaf blight of garlic; it can colonize garlic debris and develop into the sexual stage, *Pleospora allii*. This stage gives rise to black structures called pseudothecia, which ultimately give rise to ascospores that infect garlic crops in the spring. Studies in the south of Spain showed that garlic leaf debris left on the soil surface from October to December produced *c*. 6.3 pseudothecia/mm^2 of dead leaf area, whereas leaf debris buried 10 cm in the soil produced only about 2/mm^2. Moreover, pseudothecia formed on buried leaves degenerated faster than those on the surface (Prados-Ligero *et al.*, 1998). The same study showed that inflorescence stalk residues were more resistant to degradation upon burying than leaf debris and gave rise to 6.5–9.5 perithecia/mm^2, whether buried or not. The crop hygiene recommendations from this study were that it was best to gather and destroy waste seedstalks and then to plough in and bury leaf residues, in order to minimize the disease inoculum in the spring.

Crop rotation is highly desirable from a disease prevention viewpoint, so that susceptible crops do not overlap in time nearby to each other and are distanced both from each other and from the potentially diseased residues of previous crops. However, although desirable, the separation of susceptible crops in both space and time using rotation is not always economic, particularly in areas of intensive production. To reduce humidity in the leaf canopy and minimize the duration of periods of leaf wetness, thereby shortening the periods suitable for sporulation and infection, it is desirable to have widely spaced plants and a low LAI. A wide inter-row spacing with rows oriented in the direction of the prevailing wind also helps achieve this objective and is important for downy mildew control in onion seed crops. Excessive nitrogen fertilizer should be avoided, as this promotes a lush leaf canopy within which high-humidity microclimates are likely. However, low LAI reduces yield potential and delays bulb crop maturity (see Chapter 4), and green salad onions need to be grown at a high plant density to be economical. So again, practical and economic considerations may override what is optimal to minimize the risk of leaf disease.

For some leaf diseases, cultivars with disease resistance have been identified or are being developed (see Table 5.5). Most promising is the introduction of resistance from wild species, e.g. the introduction of downy mildew resistance from *Allium roylei* to onion. There is also potential to use *A. roylei* as a 'bridge species', to introduce the *B. squamosa* resistance of Japanese bunching onion *A. fistulosum* into the common onion, *A. cepa* (see Chapter 3, 'Breeding for Disease and Pest Resistance').

The surface of leaves supports a community of 'phyllosphere' microorganisms (Lindlow and Brandl, 2003). In various ways, including com-

petition for nutrients, antibiosis, degradation of pathogen cell walls, alteration of plant surface wettability, interference with pathogenicity enzymes or by triggering systemic resistance in the plant (see 'Bacterial Diseases', above), these can have an inhibitory effect on pathogenic fungi (Elad, 1996). These effects can be exploited for the biological control of leaf diseases. This has been given impetus by the widespread pressure, backed by legislation in some countries, to reduce pesticide – including fungicide – inputs in crop production. The market for organic produce, the slow and expensive development of new fungicides and the need for alternative strategies to fungicides to minimize the risk of pathogens developing resistance gives further motivation to this work.

Various fungal antagonists of leaf pathogens have been tested to control allium leaf diseases. Carisse *et al.* (2006) reported that treatment of onion plots infected with *B. squamosa* with sprays of a spore suspension of the antagonist fungus *Microsphaeropsis ochracea* reduced the number of *B. squamosa* conidia produced by necrotic leaves by 82%. Furthermore, the disease control achieved by sprays of spore suspensions of *M. ochracea* every 7–10 days was as good as that achieved by spraying the protective fungicide mancozeb with the same frequency. The antagonist also reduced the number of conidia produced by *B. squamosa* sclerotia by 75%. Sprays of *M. ochracea* spores on to onion debris after harvest could lower the number of conidia from sclerotia, thus lessening the primary inoculum for succeeding onion crops. In earlier trials, sprays of conidia of the antagonist fungus *Gliocladium roseum* (= *Clonostachys rosea*) were about half as effective as the protectant fungicide chlorothalonil in reducing leaf spots caused by *B. squamosa* (James and Sutton, 1996). *Gliocladium roseum* is a soil-dwelling antagonist and does not function as well as fungal antagonists derived from necrotic leaves in the conditions of alternating wet and dry periods typical of the leaf surface environment (Kohl *et al.*, 1995; see also antagonists and biological control of Neck rot, below).

Notwithstanding the use of good cultural and crop hygiene practices, outbreaks of leaf diseases are typical in allium-producing regions, and routine fungicide sprays are essential for control. For example, in eastern England a disease complex of downy mildew, *B. squamosa* leaf blight and *Cladosporium* leaf blotch has to be controlled. Infection by the latter two diseases can make a crop more susceptible to attack by downy mildew. Herbicide treatments that can de-wax and scorch leaves can also leave them more susceptible to disease. Any conditions that reduce leaf waxiness and cause mechanical damage to leaves are thought to increase their disease susceptibility. Leaf disease is particularly damaging to yield and storability if it occurs when onions are starting to bulb, and growers spray intensively with fungicides at this stage. Disease-free foliage is important at the late stage of bulbing if maleic hydrazide applications are to be effective for prolonging storage life (see Chapter 7).

Fungicides divide into protectants and systemics. Protectants coat the leaf surface and must be present on the leaf prior to spore germination and infection to have any benefit, whereas systemic fungicides have the potential to eradicate

the fungus after infection. The systemic fungicide metalaxyl is widely used as a systemic fungicide against downy mildew. It is always combined in a mixture with a protectant fungicide, usually either the dithiocarbamate, mancozeb or chlorothalonil, a chlorophenyl fungicide. This is to reduce the risk of metalaxyl-resistant strains of the pathogen evolving. Another strategy to reduce the selection pressure for fungicide resistance is to alternate the active ingredients used in successive fungicide treatments. Trials in the UK have found that the fungicides that are most effective can vary from site to site, depending on the prevalent diseases. In recent years control of onion downy mildew in the UK by metalaxyl has not been satisfactory, and a combination of the systemic fungicide, dimethomorph with the protectant, mancozeb has been approved as an alternative.

Onions, with their waxy, lanceolate leaves, present a difficult surface for pesticide spray retention. There has been much work carried out to improve the efficiency of pesticide deposition and to minimize run-off by using improved spray nozzles aimed and angled appropriately for the crop and by reducing spray volumes when the crop is small. This, together with more effective fungicides, has made it possible to reduce the overall fungicide application quantities in recent years, in keeping with governmental and public pressure to reduce pesticide usage. Growers still generally routinely spray every 7–10 days with fungicides while onion crops are growing, the interval between sprays depending on disease risk. Efforts to reduce the number of sprays by developing disease forecasting systems have been pursued in several countries.

The emphasis on fungicides effective for the control *B. squamosa* and other leaf blights that became prevalent in the 1970s is thought to have contributed to a revival in importance of downy mildew in The Netherlands, the UK and New York State in the 1990s, as fungicides for *B. squamosa* control were not effective against downy mildew, which had been problematic in the 1950s but well controlled with metalaxyl in the 1960s (de Visser, 2005, personal communication). Increase in the use of onion sets that can carry downy mildew inoculum over winter and that develop a large leaf canopy in which a microclimate favourable to downy mildew can occur early in the growing season is another factor that is thought to have contributed to the increasing importance of downy mildew in the UK in the 1990s. In addition, a trend toward larger fields of onions, frequently 150–200 ha in area, may have contributed to the problem. These examples show how changes in cultural practices, fungicide use and importance of various diseases interact in an ever-changing and fluid situation for allium crop disease in a growing region. A similar interactivity and fluidity applies to most aspects of agronomy, hence the need for continual monitoring, diagnosis and development work by skilled scientists and agronomists to maintain crop productivity.

With precise knowledge of the environmental conditions needed for sporulation and infection, it is possible to develop predictive models for leaf disease. Information on field microclimate can now be routinely recorded using electronic

sensors and data-loggers. This information can be used in computerized models to forecast when fungicides need to be applied to prevent disease outbreak. A good example is the model for *B. squamosa* leaf blight of onions, called 'Botcast', described by Sutton *et al.* (1986). The principal constraints to the development of this disease are periods of high temperature (> 30°C), which suppress the pathogen, and periods of low humidity and consequent lack of leaf wetness, which prevent sporulation. Based on previous studies of the epidemiology of the disease, the following algorithm was devised to predict disease severity.

1. Estimate sporulation or Daily Inoculum Value, DINOV

(DINOV = 0, no sporulation; DINOV = 1, sporulation)

Mean temperature > 30°C for > 4 h on at least one of the preceding 5 days?

→ Yes: DINOV = 0

→ No: Wetness duration on leaves in night < 5 h?

→ Yes: DINOV = 0

→ No: Wetness duration on leaves in night > 12 h?

→ Yes: DINOV = 1

→ No: RH < 70% for > 6 h on previous day and no rain or irrigation occurred?

→ Yes: DINOV = 0

→ No: DINOV = 1

Calculate Daily Infection Value, DINFV.

2. The value of DINFV for the first two nights following a sporulation (i.e. DINOV = 1) is calculated as 0,1 or 2 according to temperature and the duration of leaf wetness, as indicated by Fig. 5.14.

3. Disease Severity Index, DSI, calculated as: DSI = DINOV × DINFV.

4. Cumulative Disease Severity Index, CDSI, calculated as: CDSI = sum of DSI values from the day of onion emergence.

5. CDSI compared with two thresholds:

CDSI = 21–30, Threshold 1 – some risk of disease, apply fungicide if rain or irrigation expected

CDSI = 31–40, Threshold 2 – high risk of disease, apply fungicides as soon as possible.

Implicit in the model are the assumptions that initial inoculum is always present, that spores produced at night can survive for up to 2 days and that conditions suitable for spore dispersal occur every day.

In trials in Ontario, Canada good correlations between disease severity and CDSI were obtained, and Threshold 2 values occurred just a few days before epidemic disease increases began. By starting fungicidal sprays either at

'Botcast' Threshold 2 rather than the conventional time, when local onion growers started, disease was controlled with an average of only three sprays per year rather than seven. Similar models were developed at around the same time in New York State and Michigan, USA (Lorbeer *et al.*, 2002).

Tests of these models in western Europe have resulted in the development of 'hybrid' models. A combination of rules from both Botcast and Blight Alert, the New York model, reduced fungicide sprays by 27–78% without any loss of yield over 3 years of trials in France (Huchette *et al.*, 2005). A combination of Botcast for forecasting the initial spray and the SIV model from Michigan reduced the number of sprays required in The Netherlands by 54% compared with weekly sprays without any yield loss (de Visser, 1996). In The Netherlands and the UK, the re-emergence of downy mildew as a serious disease in the 1990s has limited the practical usefulness of predictions for spraying against *B. squamosa* since farmers needed to spray routinely with fungicides for downy mildew control (de Visser, 1998). Therefore, a predictive forecast for downy mildew control combined with one for *B. squamosa* is required.

Information relating downy mildew risk to the time and duration of temperatures and humidities conducive to sporulation and relating infection to the time and duration of leaf wetness along with suitable temperatures has been incorporated into disease-forecasting models – for example, the perhaps appropriately named 'Downcast' developed in Ontario, Canada (Jesperson and Sutton, 1987). This model correctly predicted sporulation on 111 out of 119 nights over two growing seasons in Ontario, and it also proved satisfactory in Queensland, Australia. However, the model predicted only about 50% of observed sporulation/infection incidences in The Netherlands (de Visser, 1998) and gave no better than a random prediction of sporulation in the UK (Gilles *et al.*, 2004). Suggested reasons for these failures of 'Downcast' include the highly variable weather in European maritime areas, possible differences in the conditions required for sporulation by pathogen strains from different geographic locations (Gilles *et al.*, 2004) or inconsistencies in leaf wetness measurements with the available instruments (de Visser, 1998). A modification of 'Downcast' (de Visser, 1998) gave better results in The Netherlands and enabled a 15–29% reduction in the number of fungicide applications needed in trials in France, with no loss of yield (Huchette *et al.*, 2005).

A quantitative model of spore production by downy mildew, named 'MILIONCAST', was developed in the UK, based on observations of the effects of temperature and relative humidity on numbers of sporangia produced. This gave a good prediction of observed occurrence and intensity of sporulation in test plants outside (see Fig 5.15). In Germany, the model 'Zwipero' was developed to predict downy mildew sporulation infection events using simulated inputs of temperature, humidity and leaf wetness within the onion canopy (Friedrich *et al.*, 2003). These simulated inputs were outputs from another model calculating these properties within a leaf canopy from standard weather data measured 2 m above

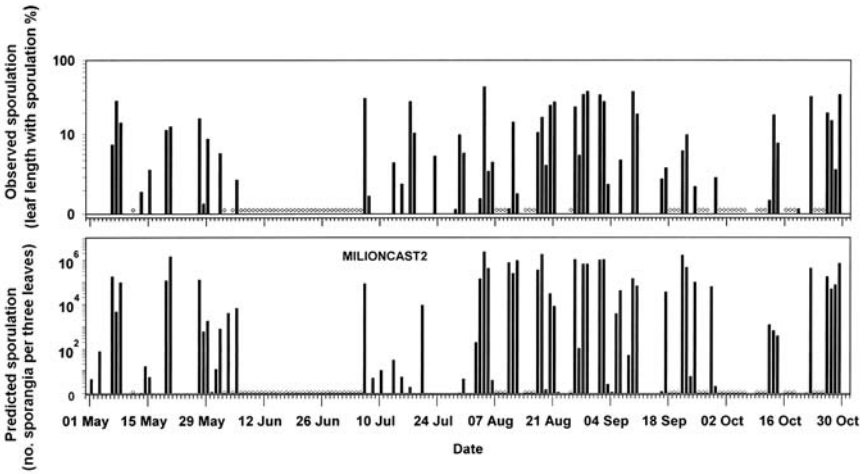

Fig. 5.15. A comparison of observed sporulation by onion downy mildew, *Peronospora destructor,* and predictions of sporulation made by the computer model MILIONCAST2 using measurements of temperature and relative humidity logged every 10 min from sensors close to the onion leaves (from Gilles *et al.*, 2004. Courtesy of *Plant Disease*).

the ground. This combination of models is being tested with forecast weather to give a prediction of sporulation/infection events a day or two in advance, rather than an estimate of their likelihood following observed microclimatic conditions.

A disease forecasting system has also been developed for purple blotch caused by *Alternaria porri* based on weather-based predictions for the production of spores and on daily hours of leaf wetness and the age-dependent susceptibility for infection of onion leaves (Lorbeer *et al.*, 2002).

Current disease risk prediction models are regarded as aids to crop management, mainly indicating when scouting for signs of disease should be intensified (Lorbeer *et al.*, 2002; Friedrich *et al.*, 2003) or when spray programmes should commence. Since most models are based on current microclimate data their sporulation infection estimates are retrospective, and protectant fungicides would be ineffective in preventing infection. However, prompt application of systemic fungicides can check downy mildew infection, and application of these following high risk predictions could ensure maximum efficacy for the limited number of such sprays that are allowed in a growing season (Gilles *et al.*, 2004).

Although microclimate-based models predict when conditions are suitable for sporulation infection, they give no indication of whether the inoculum to initiate disease is present in the vicinity of the crop. The number of leaf lesions due to *B. squamosa* was found to be linearly related to the concentration of spores in the air around the crop (see Fig. 5.16).

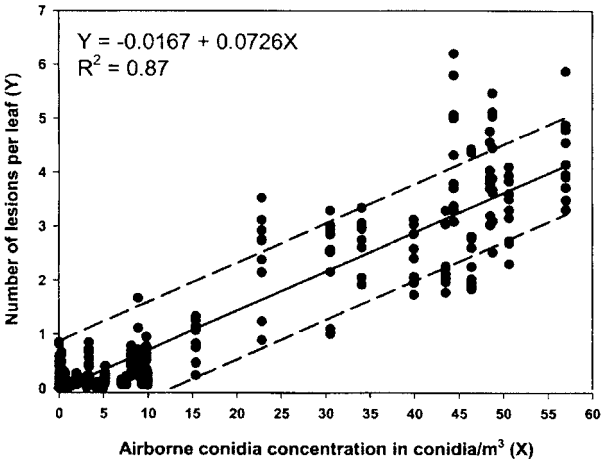

Fig. 5.16. The relationship between the number of lesions of *Botrytis squamosa* counted on onion leaves and the concentration of airborne conidia derived from spore trapping between 10.00 and 12.00 am in field trials in Quebec, Canada in 1999 and 2000. The solid line represents the linear regression and the broken lines the upper and lower 95% confidence band. An airborne inoculum concentration of 10–15 conidia/m^3 was found to be the appropriate threshold for initiating fungicide sprays to prevent the disease (from Carisse *et al.*, 2005. Courtesy of *Plant Disease*).

Spray programmes initiated only when the concentration of spores exceeded 10–15/m^3 resulted in fewer than half the number of sprays compared with a conventional routine spray programme in Quebec, Canada, with no increase in disease severity, mainly because of delays in the start of spraying (Carisse *et al.*, 2005). A technique has been developed for monitoring fungal pathogen spore concentrations using a novel spore trap to capture and quantify them by measuring colour intensity in an enzyme-linked immunosorbent assay (see Fig. 5.17). This technology makes it possible for the concentration of particular pathogen spores to be monitored within mixed-species aerial spore populations by non-experts.

By combining these improved methods of spore trapping with meteorologically based models for sporulation and infection potential, more precise forecasts of the need for fungicide sprays will be possible. Thereby, the number of fungicide applications could be reduced, with a consequent reduction in pollution, cost and risk of development of fungicide-resistant pathogens. These technologies need integrating within farm management systems. Currently, it is often regarded as easier to manage men and equipment in large farming operations using routine spray programmes rather than spraying according to disease risk forecasts where the timing of sprays is more episodic.

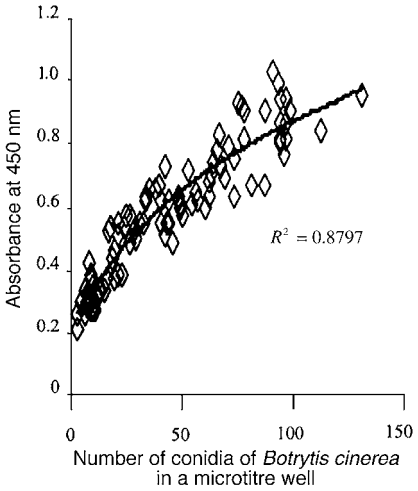

Fig. 5.17. Results from a device for the rapid detection and immunoquantification of airborne pathogen spores. The relationship between colour intensity as measured by light absorbance at 450 nm in microtitre wells of a spore-trapping device and the number of conidia of *Botrytis cinerea* trapped in the wells. The colour was developed using an enzyme-linked immunosorbent assay (ELISA) created using *Botrytis*-specific monoclonal antibodies (from Kennedy *et al.,* 2000. Courtesy of *Applied and Environmental Microbiology*).

FUNGAL DISEASES INFECTING FROM THE SOIL

There are several important soil-borne fungal diseases of allium crops that invade roots or stem bases. As with other types of pathogen, there is a range from those specific to alliums to those that attack many crop species. Entwistle (1990) has written a review and bibliography on these diseases, and they are described and illustrated in Schwartz and Mohan (2008). The diseases and their causal pathogens are listed in Table 5.6.

The root diseases of alliums all have a number of features in common. All these organisms can infect roots and most can penetrate below-ground shoot tissue and infect the stem base. Pink root is exceptional in that it is confined to roots and the dry outer sheaths of the shoot base. The symptoms of disease, as might be expected from the destruction of roots, are those associated with water or nutrient stress. Leaves lose turgor, wilt, become yellow and ultimately die, and plants become stunted and may collapse. The symptoms are aggravated by drought. Early attack can result in the failure of emergence or the collapse of seedlings.

The diseases tend to group very roughly into those of cool temperate climates and those of warmer regions, depending on their temperature requirements (see Table 5.6). However, in mid-latitude Mediterranean

Table 5.6. Fungal diseases of allium vegetables infecting from the soil.

Disease	Pathogen	Host range[a]	Temp. (optimum, °C)	Temp. (range, °C)	Control[b]
White rot (see Plates 2 and 8a)	*Sclerotium cepivorum*	All allium crops	14–18	9–24 for sclerotial germination; 5–29 for mycelial growth	Fu, so, f, at
Pink root (see Plate 8b)	*Pyrenochaeta terrestris*	O, g, s, l	24–28	⩾ 16	Rv, ro, fu, so, at
Fusarium basal rot (see Plate 8c)	*Fusarium oxysporum*; f. sp. *cepae*; f. sp. *allii*	O, g, j, r	28–32	15–32	Rv, ro, fu, so, at
Garlic and leek root and basal rot	*Fusarium culmorum*	L, g			
Southern blight	*Sclerotium rolfsii*	O, g, l, j, s and many other spp.	27–30	⩾ 15	Fu, so
Damping off	*Fusarium* spp.; *Pythium* spp.; *Rhizoctania* spp. and *R. solani*	All allium crops and many other spp.	Wide range		Fu, so, at

[a]O, onion; g, garlic; s, shallot; l, leek; j, Japanese bunching onion; r, rakkyo.
[b]Fu, fumigation; so, solarization; f, fungicide; at, avoidance by timing; rv, resistant cvs; ro, rotation.

climates, diseases of cool temperatures like white rot may attack winter crops and diseases of warmer temperatures afflict summer crops.

Changes in cultural practices can influence root diseases, often in an unexpected fashion. A good example is the effect of flood control in Egypt on white rot following the building of the Aswan dam. Previous to this, the fields used for onion production had been subject to several weeks of flooding, followed by a baking, with temperatures as high as 39°C at 5 cm, as the soil dried out. This, together with the annual deposit of fresh silt from the flood waters, prevented white rot. After floods were prevented, severe white rot led to a more than 50% decrease in winter onion production and a large decline in exports.

Further details of particular diseases

White rot

White rot is one of the most devastating and important diseases of allium vegetables. The fungus penetrates the root epidermis and invades the root

cortical tissue. Plants infected with white rot may have a cottony white or grey mass of fungal mycelium on the stem base. This mycelium can infect adjacent plants and, therefore, spread of the disease is facilitated by the high plant densities typical of salad onion production. Black resting bodies about 0.5 mm in diameter, termed sclerotia, are formed in the mycelium and on the base of infected plants. The resting sclerotia of white rot can survive for more than 18 years in field soil.

The white rot fungus is highly specific to alliums, and the germination of the sclerotia is stimulated by the characteristic volatile 'flavour' compounds around their roots (see Chapter 8). The disease can occur on all the vegetable alliums but tends to be more serious on garlic and onion than on leek. Field infections can go unnoticed at first, but can reduce yields to uneconomic level in 4 years of successive onion crops. Once established, because of the persistence of sclerotia in soil, infected land is usually abandoned for onion production.

Pink root

Infection by *Pyrenochaeta terrestris* results in characteristic pink-hued roots which become darker red with time. Infected roots ultimately collapse and die. The fungus is an important pathogen on a number of non-allium crops and can survive in soil as various types of spore or on debris or roots of susceptible crops. The pathogen produces several toxins involved in causing disease.

Fusarium basal rot

This disease is caused by *Fusarium oxysporum* f.sp. *cepae*, which is one of over 100 formae speciales (f.sp.) of *F. oxysporum*, many of which are pathogenic. Cramer (2000) has reviewed the research on this disease. The primary source of inoculum in the field is round, thick-walled chlamydospores. The pathogen can cause disease at all stages of onion growth, from seedling to stored bulb (see Fungal Diseases of Stored Bulbs, below). The fungus can penetrate the base plate of alliums and cause a brown discoloration and rot, so that the shoot easily detaches from the base. Infection can be increased by damage from pests, and the disease sometimes occurs together with pink root.

Garlic and leek basal rot

The pathogen *Fusarium culmorum* has been recognized as the cause of a rot of planted cloves, young plants and the baseplate and bulbs of garlic. The same pathogen has been identified as the cause of a root and stem base rot of leeks, which causes a reddish-purple discoloration at the base of the pseudostem. The pathogen does not cause disease on onion or shallot. The disease was first reported in garlic in California in 1976, and in leeks in Spain in 1996. Because the leek disease was found in California on seedlings growing in soil-less compost in glasshouses, it was thought likely to have originated from infected seed, and therefore to be seed transmissible (Koike *et al.*, 2003).

Southern blight

The pathogen causing this disease attacks a wide range of crops in warm climates. On onions its symptoms are dirty white spots on the outer bulb scales and neck near the soil surface; these later become water-soaked and mushy. A web of fungal mycelium may form on and around the bulb, and spherical, brown sclerotia may form on the bulb. The fungal hyphae can penetrate onion shoots directly. The pathogen can invade from plant to plant. The primary inoculum can be mycelium in infested organic matter or from sclerotia.

Damping-off disease

In common with all crops, allium seeds and seedlings are susceptible to attack after sowing and during germination, and to emergence by numerous species of fungus in the families listed under damping-off in Table 5.6. These fungi are ubiquitous in soil. Seeds are routinely film-coated with fungicides to reduce damping-off (see below). *Pythium* spp. tend to be most destructive in cold, wet soils, so good drainage helps to avoid infections. Details of the various fungal species implicated and their life cycles are given in Schwartz and Mohan (2008).

Smut and smudge

Onion smut caused by *Urocystis colchici* is a soil-borne disease, but because it manifests primarily in the shoot it is discussed in the section on Fungal Leaf Diseases. Onion smudge caused by *Colletotrichum circinans* invades bulb skins from the soil, but is discussed in the section on Fungal Diseases of Stored Bulbs, below.

Disease control

The techniques of disease control can be grouped under several headings relevant to most of these soil-borne diseases.

Prevention of spread

All soil-borne diseases can be spread by anything that moves infected soil from place to place. It is important to ensure that planting material is disease-free. Transplants, sets and cloves should be raised on non-contaminated land and, if necessary, inspected for freedom from disease. The movement of contaminated soil from disease-infested land on boots, implements, etc. must be prevented. Infected plant debris should be confined and the disease propagules destroyed by high-temperature composting (Coventry *et al.*, 2002) or other means.

Cultural control

Crop rotation can be effective for the control of those root diseases with fairly short-lived propagules. A 5- or 6-year gap between allium crops is effective for

pink root control in Idaho, USA, and a 3 or more-year gap is recommended for *Fusarium* basal rot control in Colorado, Tasmania and the Philippines. The pathogens responsible for pink root, *Fusarium* basal rot and southern blight all have a wide host range, and non-susceptible crops should be rotated with onions. However, some soil-borne pathogens have extremely long-lived resting bodies – in particular, the sclerotia of white rot, so that control by rotation is not an option.

The development of disease is dependent on temperature (see Table 5.6), and it is sometimes possible to avoid root disease by growing allium crops at the times of year when soil temperatures do not favour disease. For example, in Israel early onion cultivars produce mature bulbs before soil temperatures rise above 25°C and favour pink root, southern blight or *Fusarium* basal rot. In Louisiana, USA, shallots planted in August, rather than the usual September–October, can be harvested in November, before soil temperatures decrease to the range at which white rot becomes a problem. In the UK, overwintered salad onions can be harvested in April, before soil temperatures rise sufficiently for white rot outbreaks.

With the damping-off diseases, infection risk is minimized by shortening the time that plants are in the vulnerable seedling stage. This can be achieved by sowing when temperatures favour rapid emergence and growth, and by providing good seedbed conditions.

Resistant cultivars

There is a long history of breeding onions for resistance to pink root in the south-eastern USA, and cultivars with a fair degree of tolerance have long been grown there. Resistance appears to involve both the capacity of roots to resist infection and the capacity to produce new roots after infection (Entwistle, 1990). True resistance needs to be distinguished from situations where early maturity allows a cultivar to avoid temperatures conducive to the disease. The situation is similar for resistance of onions to *Fusarium* basal rot (FBR): resistance to the disease is not absolute, but losses are greatly reduced. Numerous techniques of screening for resistance have been developed, including seedling tests. Resistance to FBR was found to be highly correlated with resistance to pink root in one population (Cramer, 2000). There remain some regions where photothermally adapted cultivars resistant to pink root and FBR still need to be developed. Despite considerable research efforts worldwide, reliable resistance to white rot has not yet been identified (Hovius *et al.*, 2005).

Destruction of propagules

There is often a correlation between the population density of pathogen propagules in soil, which is termed the inoculum density, and the severity of disease. There are a number of measures which reduce inoculum density – crop rotation discussed above being one – and others are now considered.

FUMIGANTS Pathogen inoculum can be destroyed by soil fumigants like methyl bromide, chloropicrin or dichloropropene. Although expensive, this is effective against a wide range of root diseases (Sumner *et al.*, 1997). Sealing the soil surface with polythene sheeting after application retains the fumigants within the soil for longer and increases their effectiveness (Entwistle, 1990). Fumigation has been used to eliminate small foci of white rot infection or to produce seedbeds free of *Fusarium* basal rot for raising transplants. However, the use of fumigants is becoming increasingly unacceptable on environmental grounds; in particular, methyl bromide has been identified as an ozone-depleting substance and is being phased out (Clarkson and Whipps, 2002).

SOIL HEATING In hot countries, solarization (see Nematode Pests, above) acts similarly and destroys pathogens in the top 25–30 cm of soil by raising temperatures by 10–15°C (Clarkson and Whipps, 2002). For example, in southern Spain covering wet soil with a thin film of polythene for 8 weeks starting in July reduced the number of white rot sclerotia from 100 to 150/kg of soil to undetectable levels and doubled garlic yields in white rot-infested plots (Prados-Ligero *et al.*, 2002). Solarization is effective only in regions with high insolation; for example, in a cool summer in Victoria, Australia, solarization did not suppress pink root disease but it did increase yields and improve the preventative effect of the fumigant dazomet on the disease (Porter *et al.*, 1989). In cool climates steam can be used to heat-sterilize soil and destroy root-infecting pathogens, but it is expensive and feasible only on a small scale for eliminating infection 'hot spots' or for producing disease-free beds for transplant raising (White *et al.*, 2000). Land treated with solarization or fumigants can be fairly rapidly reinfected from nearby soil or by pathogens which have survived deep in the soil (Porter *et al.*, 1989; Prados-Ligero *et al.*, 2002).

PATHOGEN GERMINATION STIMULANTS One interesting, biologically based technique is the application of chemicals that stimulate propagule germination in the absence of host plants, and this approach has been tested with some success against white rot. The sclerotia of *Sclerotium cepivorum* are stimulated to germinate near allium roots by the characteristic 'flavour volatiles' (see Chapter 8) resulting from the exudation of precursors into the rhizosphere. If host plants are absent after it germinates, the pathogen dies. Onion oil and the flavour volatile diallyl disulfide (DADS), which can be produced chemically, stimulate the germination of white rot sclerotia. In field trials on organic soils in Ontario, Canada, injection of 85.5% DADS at a rate of 10 l/ha in 500 l/ha water reduced white rot incidence in bulbs at harvest to negligible levels in plots which, untreated, produced 2–8% incidence but, on a site with higher disease incidence, there was no suppression of the disease (Hovius and McDonald, 2002). Greenhouse trials showed that application of DADS to the soil resulted in 80% destruction of sclerotia in 2 months compared with 100% survival in untreated soil. A similar but less marked effect of DADS on sclerotial survival was observed in

the field. The variability of these results reflect earlier reports in which DADS or onion oil applied to infected fields lowered subsequent white rot incidence by up to 75%, but in other trials they were not effective (Entwistle, 1990).

COMPOSTS AND CROP RESIDUES Considerable volumes of onion waste are generated from packhouses and food-processing factories. The knowledge that white rot sclerotia are stimulated to germinate by flavour volatiles prompted research into using such processing waste as a cheap soil amendment, which contained such volatiles and could be used to destroy sclerotia.

Experiments established that sclerotia in onion waste are destroyed by 3 days at temperatures of 48°C and above, so this was the minimum treatment needed to avoid spreading disease from infected waste (Coventry *et al.*, 2002). Pot experiments have shown that sclerotial destruction does occur in soil treated with such composts, but a high ratio of compost to soil is needed for much effect. For example, compost produced in 7 days at 54°C caused more than 60% destruction of sclerotia in a 50:50 soil:compost mix kept at 13°C for 6 months. Although the composted waste contained flavour volatiles, there was evidence that the destruction of sclerotia by compost was due to other factors in addition. Further experiments showed that composts from brassica or carrot waste had a similar effect, although onion waste was the most effective (Coventry *et al.*, 2005).

Fungicides

Fungicidal treatments for soil-borne diseases are difficult, because roots and stem bases are inaccessible to chemicals. It is usually only at seed sowing, set or bulb planting or seedling transplanting that fungicides can be placed where they are going to be most effective. The broad-spectrum dithiocarbamate protectant fungicide, thiram, combined with systemic, curative fungicides like thiobendazole or carboxin, is routinely applied as film-coats to allium seeds (Taylor *et al.*, 2001). This treatment reduces losses to the damping-off diseases. Fungicidal dips can be applied to garlic cloves, onion sets and transplants and can give protection against *Fusarium* basal rot (Cramer, 2000).

Selective systemic fungicides have proved effective for white rot control. Currently, the systemic fungicide tebuconazole is very effective (Melero-Vara *et al.*, 2000; Wood *et al.*, 2002; Clarkson *et al.*, 2006). A seed-coating containing 5 g of tebuconazole/kg of seed reduced the incidence of white rot on bulb onions harvested from a white rot-infected field from 47% for untreated controls to 9% for the seed treatment (Clarkson *et al.*, 2006).

Similarly, trials on garlic showed that dipping cloves in a tebucanazole solution before planting reduced infection with white rot, and this treatment plus four sprays of the fungicide solution aimed at the stem base increased bulb yield by 33% and reduced the number of plant deaths from 17 to 1.5% (Melero-Vara *et al.*, 2000). This treatment was as good as solarization in overcoming white rot. As with many fungicides, there is some phytotoxic effect of

tecnobucazole, and the emergence percentage and early plant size from seeds and onion sets decreases as the concentration applied in seed-coats and set dips increases. The best compromise between these reductions in vigour and control of white rot was to use 0.4 g of tecnobucazole per 10^5 seeds and to dip onion sets in a 1.25 g/l solution for 20 min (Wood *et al.*, 2002). Experiments combining tecnobucazole seed treatment with the biological control agent *Trichoderma viride* have given enhanced control of white rot compared with either treatment individually, showing that the two approaches to disease control are not necessarily incompatible (Clarkson *et al.*, 2006).

In the 1980s the dicarboximide fungicide iprodione was effective for the control of white rot and was used in targeted application methods, including seed-coating, stem base sprays, incorporation below the seed at sowing and incorporation in compost for seedling production (Entwistle, 1990). After several years, iprodione ceased to be effective for white rot control. The same had occurred some years previously with dichloran. The cause of these failures was the selection and build-up in soil of bacteria that rapidly degrade the fungicides, a phenomenon termed 'enhanced degradation' (Entwistle, 1990). Enhanced degradation has proved long-lasting and irreversible on a practical field scale.

Biological control

The increasing concerns about chemicals in the environment, plus problems of loss of fungicidal activity through the build-up of resistance and of enhanced degradation in soil, have encouraged efforts to develop alternative, biologically based systems to control root disease. There are many examples of bacteria and fungi exerting control against rhizosphere pathogens through a number of mechanisms, including competition and exclusion, antibiosis, parasitizing the pathogen (hyperparasatism) and inducing host resistance (Whipps, 2001).

Quite a number of such fungal antagonists have been identified, including strains of *Sporidesmium sclerotivorum*, which destroy white rot sclerotia, and *Trichoderma harzianum*, which attacks both the hyphae and sclerotia of white rot. The latter fungus has been applied to a growing crop in trials in Egypt, and has reduced disease (Entwistle, 1990). Cultures of *T. koningii* applied around onion seeds at a rate equivalent to 1590 kg/ha reduced the proportion of seedlings infected with white rot by about 70% (Metcalf *et al.*, 2004). Compost inoculation with *T. viride*, or dipping transplant roots in a suspension of the fungus, reduced pink root disease in leeks (Biesiada *et al.*, 2004). On the other hand, applying a culture of *T. harzianum* below garlic cloves at planting or dipping cloves in a suspension of the bacterial antagonist *Bacillus subtilis* had only a slight effect on white rot disease (Melero-Vara *et al.*, 2000).

The general experience with microbial antagonists has been that the control achieved is erratic and unpredictable under field conditions. Improvement in this situation is only likely to come about through the better understanding of biological processes in the rhizosphere. Successful biocontrol agents need not

only to be antagonistic to pathogens *in vitro* but to be effective also in the rhizosphere environment (Whipps, 2001).

At the start of a programme to identify biocontrol agents that destroy white rot sclerotia and to investigate factors affecting their activity, Clarkson *et al.* (2002) identified 65 fungal isolates that could destroy white rot sclerotia on agar. Fifteen of these degraded sclerotia in soil and 16 controlled white rot disease in seedling assays. From these tests two isolates of *T. viride* were selected as most promising. In field trials on heavily infected soil, infected bulbs were reduced from 75 to about 50% by the application of these – cultured in bran and suspended in a gel – below seeds at sowing and to the base of plants during growth. Further studies on these antagonists established how soil temperatures, water potential (see Fig 5.18) and soil type influenced sclerotial destruction. Sclerotia were destroyed by the antagonists in all soil types and they were clearly active in the range 15–18°C, temperatures optimal for white rot infection of onions. However, the degree of white rot control in seedling bioassays using the selected strains still varied with soil type and against different isolates of the pathogen (Clarkson *et al.*, 2004).

Improved disease control amounting to its virtual elimination was achieved in some glasshouse trials by combining *T. viride* inoculation with growing seedlings in a combination of 50:50 soil:composted onion waste, or by com-

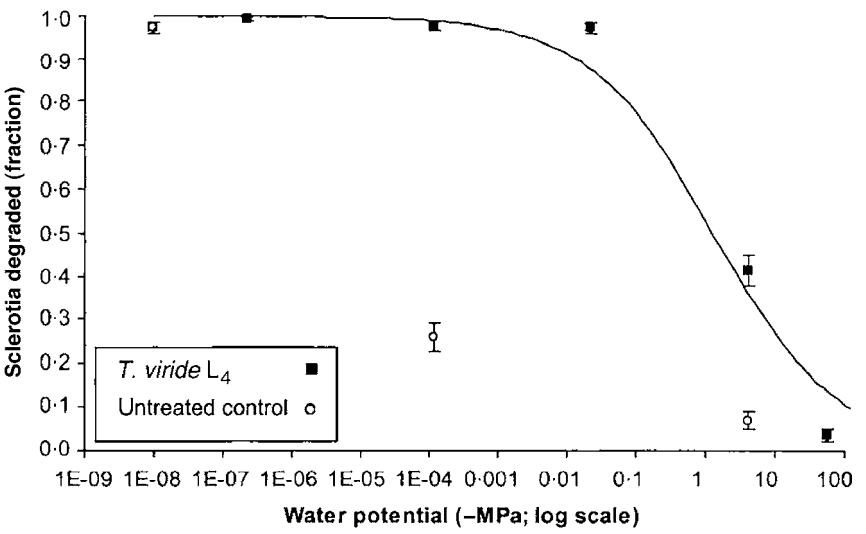

Fig. 5.18. The effect of soil water potential on the degradation of white rot (*Sclerotium cepivorum*) sclerotia by a strain of the antagonistic fungus *Trichoderma viride* selected for its virulence. The bars around the points show standard errors, and the line was fitted by regression (from Clarkson *et al.*, 2004, Fig. 1a. Courtesy of *Plant Pathology*).

bining *T. viride* inoculation with a tecnobucazole seed treatment (Clarkson *et al.*, 2006). It may be that biological control agents, disease-suppressive composts and fungicidal seed treatments can be combined to give improved control of white rot in future.

FUNGAL DISEASES OF STORED BULBS

Basic information on the most important fungal diseases of stored bulbs is summarized in Table 5.7. The information in this section is largely drawn from Maude (1990b), Snowdon (1991) and Mohan and Schwartz (2008).

Sometimes, some of the pathogens discussed under soil-borne fungal diseases do not manifest as disease until they cause rots in stored bulbs. These include: (i) *Fusarium oxysporum*, which can cause watery softening advancing from the base of the bulb, sometimes with a pink tinge; (ii) *Sclerotium rolfsii*, where infections late

Table 5.7. Main fungal diseases of the stored bulbs of allium vegetables.

Disease[a]	Pathogen	Host crops[b]	Characteristic symptoms	Infection sources	Temperatures: range; optimum (°C)
Neck rot (see Plates 2, 9a and 9b)	*Botrytis aclada*; *B. allii*; *B. byssoidea*	O, s, g, l	Bulb decay starting at bulb neck, forming black sclerotia on bulb surface	Spores from senescent leaves and from sclerotia; infected seed	5–25; 22–23
Black mould (see Plate 9c)	*Aspergillus niger*	O	Black, sooty mould on and between outer bulb scales, particularly along veins	Debris in soil; infected seed	10–40; 28–34
Blue mould	*Penicillium* spp.	O, g	Soft, watery lesions later covered with blue mould	Debris in soil	15–32; 21–25
Smudge (see Plates 2 and 9d)	*Colletotrichum circinans*	O, s, l	Black, bristled spots on surface of white-skinned bulbs	Spores splashed from infected debris in soil	10–32; 13–25

[a]The diseases are listed in order of importance.
[b]O, onion; s, shallot; g, garlic; l, leek.

in growth may escape detection at harvest and will cause the bulbs to soften and rot in store unless kept cool; (iii) *S. sclerotiorum*; and (iv) bulbs infected with *S. cepivorum* (white rot) may continue to rot in store. Among the foliage-infecting pathogens: (i) *Alternaria porri* can sometimes cause a watery rot starting in the bulb neck, which is initially yellow but then becomes purple-red; (ii) *B. squamosa* can cause neck rot in white onion bulbs; and (iii) *B. cinerea* can produce a disfiguring brown stain on the skins of bulbs, but causes no internal rot.

Other minor diseases of stored bulbs reported include: (i) *Diplodia* stain, a grey to black discoloration of the skins of white onions and garlic in Texas caused by *Lasiodiplodia theobromae*; (ii) mushy rot caused by *Rhizopus microsporus*, which is geographically widespread but infrequent; and (iii) yellow mould rot, caused by *Aspergillus alliaceus*. The latter, like *A. niger*, develops in warm storage (28–32°C) and produces a mass of yellow spores and black resting bodies (sclerotia). Infection of outer bulb scales by *Fusarium proliferatum* has been shown to cause a salmon pink discoloration of the dry outer scales of white onions in Idaho and Washington State, USA (du Toit *et al.*, 2003).

Many of these potential pathogens are widespread, growing as saprophytes and sporulating on decayed matter in soil. Wounds in bulbs or necks are required for entry by many of them, and damage when onions are topped and harvested is a vulnerable stage for infection. Rapid drying of wounded necks and tissue can reduce the infection risk. The temperature optima for development of these pathogens are indicative of the regions and climates in which they are important diseases (Maude, 2006). For example, neck rot is a serious problem in temperate regions but not in warm climates, whereas black mould is commonplace in the tropics but rare in temperate conditions unless prolonged high temperatures are used to dry onion bulbs. The climatic conditions favourable to the soil-borne and foliar infections that can also cause bulb disease are indicated in the sections on these two classes of pathogen.

Neck rot

Neck rot, as its name implies, causes a soft rot in the neck and upper regions of infected bulbs. A black mass of sclerotial resting bodies often develops below the dry outer skin on the decaying tissue. A grey, sporulating mould may also develop on the surface of the decaying, fleshy scales. The symptoms usually develop some 2–3 months after the apparently healthy but infected bulbs are placed in store. Two pathogens, *Botrytis aclada* (often termed *B. allii*) and *B. byssoidea*, are exclusively associated with neck rot, the former with sclerotial and the latter with mycelial neck rot.

Two subgroups of *B. aclada* have been distinguished, one (type AI) with 16 chromosomes and the other (type AII) with 32, the latter group also having larger conidia. DNA sequencing has indicated that type AII arose as a hybrid

between AI and *B. byssoidea* (Yohalem *et al.*, 2003), and these authors have suggested that the name *B. allii* be used for the hybrid. Occasionally, the leaf pathogen *B. squamosa* causes neck rot on white skinned-bulbs. A sensitive diagnostic method has been developed to distinguish between the three pathogens that cause neck rot exclusively, and also *B. squamosa* and *B. cinerea*. This method is based on characteristic restriction enzyme fragments of DNA from a PCR-amplified section of DNA derived using primer sequences selective of DNA regions that differ between these various *Botrytis* species (Nielsen *et al.*, 2002). The technique should facilitate studies on the epidemiology of the pathogens and on the extent of seed contamination and infection by them.

The pathogens produce spores on dead leaf tissue, and these can invade the senescent tissue that occurs at the tip of ageing onion leaves. The fungus then spreads down the leaf into healthy tissue. It is latent in live green leaves, causing no disease. By sequentially invading successive leaves when they start to senesce, the pathogen ultimately enters those leaves which swell at the base to form the outer fleshy scales of the bulb. It then remains symptomless in the bulb for many weeks after harvest. Infection may also enter the bulb neck at harvest time if flail-damaged neck tissue is exposed to spores, but such infection is minimized by rapid drying of the necks after harvest (see Chapter 6). There is no evidence of spread from bulb to bulb in store, and trials have shown a one-to-one relationship between the number of bulbs rotting in store and the number of infected plants present at harvest. The apparently progressive increase in the number of bulbs that rot in store is simply the result of differences in the time to start rotting between individual pre-infected bulbs.

The pathogens also invade inflorescences of onions and cause flower and umbel blight, which can result in seeds superficially contaminated or deeply infected. In a survey of seed production in the semi-arid inland regions of Washington State, USA, where about 20% of the world's onion seed is produced, the majority of onion seed-lots produced were contaminated with *B. aclada* and, of these, most carried a low percentage of seeds with a deep-seated infection that could not be destroyed by surface sterilization (du Toit *et al.*, 2004). Umbel and flower infection occurred after the spathe had opened and had begun to senesce and the florets had opened. The proportion of infected mother plants increased during the growing period and nearly all were asymptomatically infected with *B. aclada* at flowering time, but there was no apparent relation between plant infection and infection of harvested seeds. Infections were thought to enter seed crops from the abundant airborne inoculum produced by nearby bulb crops, volunteer plants, cull piles and debris.

The discovery that the disease was seed-borne proved crucial for its control in the UK in the 1970s. By applying a coating of the systemic benzimidazole fungicide, benomyl to seeds (1 g AI/kg seed), infection of the cotyledon from inoculum on the seed-coat is prevented. Seed was the primary source of infection that was resulting in annual losses of 15–50% of the stored bulb crop. Using this well-targeted treatment, annual losses from neck rot were reduced to negligible

percentages. For an outlay of a few thousand pounds for seed treatment, millions of pounds worth of onions were saved from rotting. Trials showed that the percentage of infected bulbs at harvest was directly proportional to the percentage of infected seed seeds sown. However, a given percentage of infected seed results in a higher percentage of infected bulbs in a wet growing season than in a dry season (Maude, 2006). High humidity during the season of leaf growth favours spread from leaf to leaf and, therefore, from plant to plant.

Sprays of spores of the competitive antagonist fungus, *Ulocladium atrum* prevented sporulation of *B. aclada* on dead onion leaves and remained effective even if the leaves were dried periodically. The antagonist, therefore, shows promise as a biocontrol agent for slowing secondary infection from leaf to leaf. However, *U. atrum* did not prevent the asymptomatic spread of the pathogen from necrotic leaf tips into adjacent healthy leaf tissue (Yohalem *et al.*, 2004).

The importance of seed as the primary source of inoculum remains controversial, and probably depends on the prevalence of other sources of inoculum in the locality (du Toit *et al.*, 2004). Spores may also emanate from infected debris in soil or in dumps of onion waste: sclerotia can survive for more than 2 years in such environments. Infected crops that overlap in time with newly sown crops are another potential 'infection bridge' for the pathogen. Such an overlap often occurs where spring- and autumn-sown onions are grown together in the same locality. Infected onion sets which survive storage could be a source of disease. The disease cycle is illustrated in Fig. 5.19.

The neck rot pathogens are rapidly destroyed by temperatures of 30°C or above. Therefore, if onions are topped in the field, they should be quickly taken into store and sealed at the neck by blowing warm air over the bulbs to destroy any inoculum invading the neck. The pathogens cannot infect dry, senescent leaf tissue, so that in dry climates, onions field-dried with the foliage intact are not at risk. Treatments with fungicidal foliar sprays or fungicidal treatments to harvested bulbs are not effective in disease control.

Black mould

In tropical regions where onions are frequently stored above 30°C, the fungus *Aspergillus niger* commonly blemishes stored bulbs. This fungus invades via the neck, often via injured tissue when tops fall or are cut near maturity. Fleshy scales can be infected if the dry, outer skin of the bulb is damaged. The infected scales develop a white fungal mycelium on which sooty, black sporing bodies (conidiophores) develop. The optimum temperature for the invasion and growth of this pathogen is 32.5°C. Mould development on onion bulbs is favoured by humidities of 80% or more in the store. Except on wounded bulbs, the black, sporulating areas may be confined to the outer, fleshy scales immediately below the dry skins. The fungus may occur in association with bacteria that cause soft rot of bulbs (see Bacterial Diseases, above).

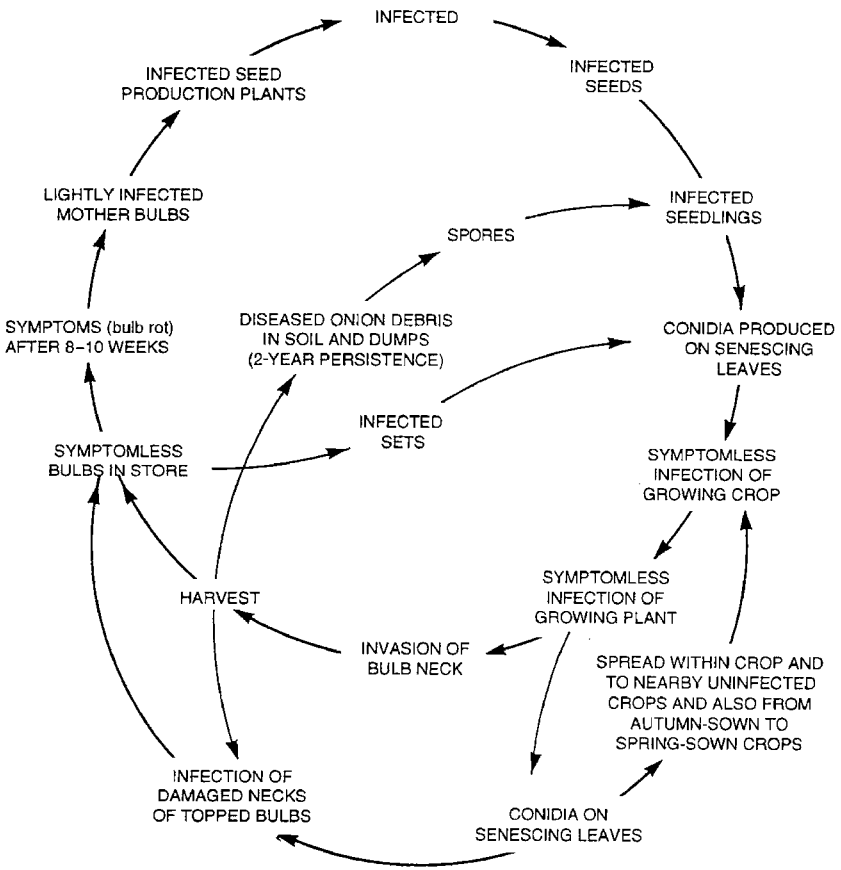

Fig. 5.19. The infection cycle for *Botrytis allii,* the cause of neck rot in stored onions.

In warm regions where onions are grown, *A. niger* can be found on onion seeds and sets, on onion foliage and on many kinds of organic debris in soil. The disease can be transmitted by seed, and the hotter the climate where seeds are produced the higher tends to be the percentage of infected seed (Maude, 2006). In trials in Sudan, dusting of seeds with the fungicide benomyl was effective for reducing bulb infection in soils where onions had not previously been grown, but in locations regularly used for onion production other sources of infection made seed treatment less effective (Hayden *et al.*, 1994). Fungicidal dips and dusting of bulbs with calcium carbonate reduce black mould, as can treatment with hydrogen peroxide (Afek and Orenstein, 2003). The growth of the fungus is slow at temperatures below 15°C and at low humidities.

Aspergillus fumigatus and *A. alliaceus* have also been reported as causing disease on onion bulbs subjected to high temperature in store.

Blue mould

Various species of *Penicillium* can cause yellowish blemishes and watery soft spots on bulbs, followed by a blue-green mould of spore-producing conidiophores on the infected surfaces. Blue mould is a serious storage disease of garlic in California. Infected cloves soften and shrivel and can ultimately become a mass of blue-green spores. These fungi grow commonly on organic debris in soil and on senescing plant tissue. Invasion of bulbs is usually through tissue damaged by bruises, wounds, sunscald or freezing.

The *Penicillium* species that can cause bulb rots have now been classified as a group of seven species within the *Penicillium* series *Corymbifera*, one of which, *P. allii*, is the predominant pathogen of garlic and onion (Overy *et al.*, 2005a). Unlike most of the ser. *Corymbifera, P. allii* fails to produce plant cell wall-degrading enzymes at temperatures below 15°C (Overy *et al.*, 2005b), and therefore disease can be prevented by low-temperature storage. Disease control involves careful bulb handling to avoid damage, and storage at temperatures of 5°C or less at humidities as low as possible to avoid shrivelling. However, five others among the seven species in ser. *Corymbifera* can cause a rot in the base plate of yellow onions, and they can produce cell wall-degrading enzymes at 5°C; therefore, they have potential to cause disease in cool storage (Overy *et al.*, 2005a, b).

Penicillium allii (formerly called *P. hirsutum* (Overy *et al.*, 2005b)) can also weaken or kill recently planted garlic in the field. When infected bulbs are separated into cloves for planting, these can be infected via wounds created in the process. To minimize infection, cloves should be planted as soon as possible after separation. Differences in susceptibility have been found between Argentinean garlic cvs (Cavagnaro *et al.*, 2005).

Smudge

Onion smudge, caused by *Colletotrichum circinans*, is a soil-borne disease that causes green-black dots on the skin of white onions (see plate 9d) and yellow, watery cratering of the underlying fleshy tissue. Cultivars with coloured skins are rarely affected because their skins contain protocatechuic acid, which makes them resistant to smudge (see 'The Skin of Onion Bulbs' in Chapter 7). Black resting bodies called stromata remain viable for many years in soil. These can germinate and produce acervuli, which produce conidia. Conidia germinate to produce an appressorium via which the pathogen can penetrate the plant cuticle. Acervuli are circular spots producing spores and are surrounded by characteristic bristles, which can be seen with a hand lens. The infection is spread by rain-splash from infected soil. Humid conditions and temperatures of 25°C enable the pathogen to progress from infection to sporulation within a few days. Rapid drying after harvesting bulbs is helpful for control, but white-skinned varieties should be avoided where the disease is prevalent.

MYCORRHIZAL FUNGI

The roots of alliums are frequently colonized by fungi of the family Endogonaceae. The hyphae of these fungi penetrate between the cells of the root cortex and extend into the soil. Within the root the hyphae form branched appendages that penetrate the host cell walls, but remain outside the cytoplasmic membrane of root cells. Globules of dense cytoplasm accumulate around these invaginations, forming characteristic tree-shaped microscopic structures termed 'arbuscules' (see Fig 5.20b). Hence, these fungi are termed arbuscular mycorrhiza (AM). Arbuscules are thought to be where the fungus and plant exchange nutrients. Dense, oil-rich globules or vesicles are also formed between root cells by the fungus (see Fig 5.20c).

AM fungi infect the roots of most plant species, with no marked specificity, and occur naturally in soils worldwide. The review by Stribley (1990) of the significance of AM for allium crops is the basis for much of this brief account. More recently de Melo (2003) reviewed research on AM and allium crops, with particular emphasis on their potential role in organic production. These two reviews have extensive bibliographies of the original research on the subject.

Alliums have been used in many studies on AM because of their simple roots and responsiveness to infection. The association can be of mutual benefit to both fungus and plant – in other words, symbiotic. The most important benefit to the plant is increased phosphate (P) uptake, whereas the fungus gains a supply of carbon metabolites from the host. Alliums have thick, little-branched roots, and hence a low ratio of root length to shoot weight, and they also lack root hairs. Both these features make them poorly adapted to absorb nutrients present in low concentration in soil. Phosphate exists in low concentration in the soil solution and is strongly adsorbed to the solid phase of soils. As a consequence, the transfer of P from soil to plant is frequently limited by the rate of diffusion to the root surface, especially in soils of low available P concentration. The P uptake per unit length of mycorrhizal onion root can be increased fourfold over non-infected roots because the external hyphae extend the absorbing surface. In low-P soils this can cause big increases in plant growth rate: in one trial it was estimated that infection by mycorrhiza was equivalent to 250 kg/ha of phosphate fertilizer.

Increases in photosynthetically fixed carbon exported to roots of about 7% in mycorrhizal, as opposed to non-mycorrhizal, leek plants have been measured, and this gives an indication of the 'cost' to the host plant in terms of carbon assimilates of the association (Snellgrove *et al.*, 1982). In soils of low P status the benefits to the plant in terms of the extra growth promoted by greater P uptake outweighs this 'cost' of AM association, but in high-P soils it can slow growth rate and lower maximum yields (Morgan *et al.*, 2005). However, root colonization by AM fungi is slow on plants of high P status and this may reduce the 'cost' to the plant in these conditions. AM infection may also increase the uptake rate of micronutrients present in limiting quantities in

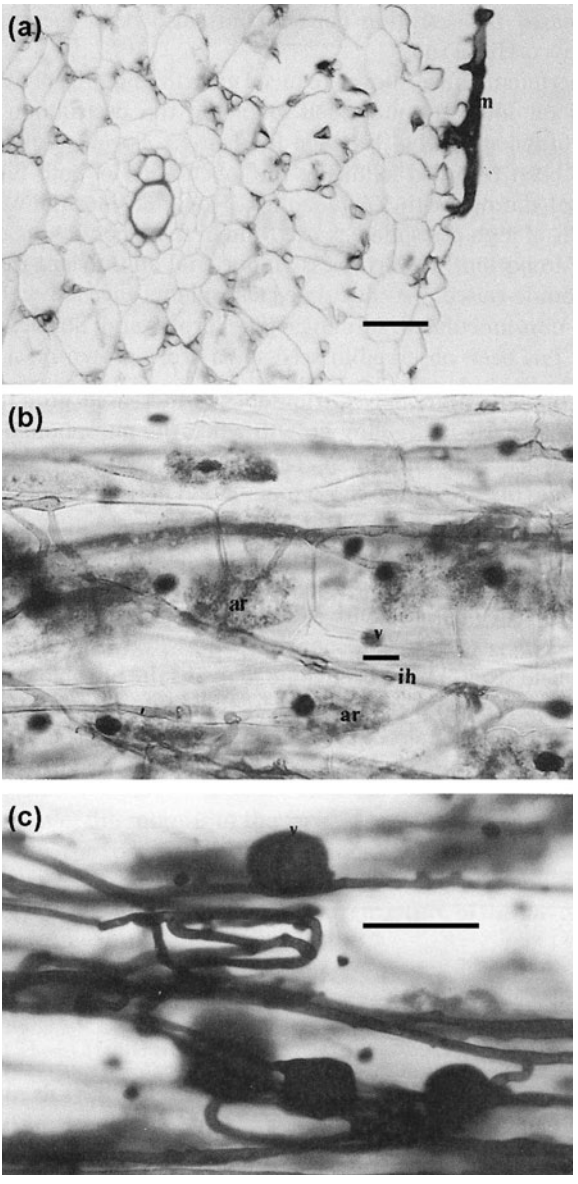

Fig. 5.20. A root of leek colonized by the mycorrhizal fungus *Glomus mosseae*. The root has been cleared with potassium hydroxide (KOH) and stained with Tryptan blue. (a) Transverse section showing external mycelium (m) attached to the root surface. (b) Longtitudinal section showing vesicles (v), arbuscules (ar) and internal hyphae (ih). (c) Vesicles (v) at greater magnification. Scale bar = 100μm (photographs courtesy of Dr F. Amijee).

soil. This has been demonstrated for copper. Increased transpiration capacity has also been measured in leek plants with mycorrhizal roots.

The symbiosis of plants and AM fungi dates from the earliest stages of land plant evolution, and even pre-dates the evolution of true roots (Raven *et al.*, 2005). The extent of the ramification through soil of the external hyphae of AM and other types of mycorrhizae and their importance in the biogeochemical cycling of mineral nutrients, have gained increasing recognition in recent years (Read and Perez-Moreno, 2003; Leake *et al.*, 2004). The meagre root system of allium crops (see Chapter 2) is almost certainly inherited from wild ancestors that were in symbiosis with AM, which increased the nutrient-foraging capacity of their roots. Some spectacular increases in growth of both directly sown and transplanted allium crops have been recorded following root inoculation with AM in low-P soils.

However, the relevance of all this to modern allium vegetable production has been questioned (Stribley, 1990; Ryan and Graham, 2002). These high-value crops are normally grown in soils rich in P, and since fertilizer inputs as a whole represent only about 5% of variable production costs (Nix, 2006), farmers have little incentive to risk loss of yield by failing to maintain soil P at a level sufficient for maximum yield. Nevertheless, several reports indicate that AM do give significant benefits in some allium production situations. In Israel, the destruction of native soil AM by solarization or methyl bromide fumigation (see 'Root Diseases') lowered chive yields on commercial farms, but yields could be restored and even increased by transplanting seedlings inoculated with AM (Wininger *et al.*, 2003). In soils of moderate to high P status in Denmark, leeks sown in soils which had previously grown crops or green-manures that were hosts to AM had higher initial P uptake, faster seedling growth and faster root colonization by AM than leeks sown following rotational pretreatments that lowered soil AM populations – for example, after brassicas, which are non-mycorrhizal (Sorensen *et al.*, 2005). On nutrient-rich peat soils in the UK, module-raised, AM-inoculated onion transplants gave fewer thick-necked plants than non-inoculated seedlings (Snellgrove and Stribley, 1986). A similar effect was observed in a P-rich soil with direct-sown onions given ammonium phosphate liquid 'starter fertilizer' (see Chapter 6), and this was attributed to increased seedling growth rates acting via the chain of causation shown in Fig. 4.33.

The significance of AM for allium crop production may increase in future. First, because there is a growing demand for 'organic' vegetables in some countries and, in this production system, soluble P fertilizers are banned; consequently, soil under organic management tends towards lower levels of available P (de Melo, 2003). Secondly, in conventional agriculture there is increasing emphasis on developing lower input and more 'sustainable' production systems (Sorensen *et al.*, 2005) in order, among other things, to minimize water pollution from P-rich soils. Thirdly, sources of readily available fertilizer P are finite and may become more expensive and in short supply in

future (Vance *et al.*, 2003).

For these reasons there is research on techniques of utilizing AM for producing satisfactory yields of allium vegetables on soils lower in readily available P than the current norm. In addition to the potential for improved P uptake, root colonization by AM fungi can suppress root diseases (Whipps, 2004), possibly even allium white rot (Torres-Barragan *et al.*, 1996), and may increase resistance to soil salinity and water stress as well as improving micronutrient uptake (Stribley, 1990; de Melo, 2003). The hyphal networks of AM fungi help to stabilize soil structure, particularly under soil management systems where they are not disrupted, i.e. in low- or zero-tillage systems (Ryan and Graham, 2002).

These additional potential benefits give further impetus for research to develop systems of utilizing AM associations by allium crops. Among the interesting developments is the co-inoculation of onion transplants with AM fungi and phosphate-solubilizing bacteria. Seedlings so treated were able to extract a greater fraction of their P uptake from the non-exchangeable fraction of soil P or from sparingly soluble rock phosphate, a form of P fertilizer permitted to organic farmers (Toro *et al.*, 1997). Crop rotations and break crops which maintain high populations of native AM in soil and are of potential benefit to leek crops have been designed (Sorensen *et al.*, 2005). There are several reports of increases in both growth rate and yield of Japanese bunching onions, *A. fistulosum*, following inoculation with AM (de Melo, 2003).

The effects of growing media – including different types of peat and rockwool, species of AM inoculum and P concentration in liquid feed on growth and root AM colonization percentage – have been studied for transplant seedlings of *A. fistulosum* raised in modular cells (Matsubara *et al.*, 2002). The best results were from sowing seeds in 13 ml cells with 0.5 g inoculum of *Gigaspora margarita* in a growth medium of brown peat and vermiculite (9:1, v/v) fertigated initially with 1 ml per cell of a complete nutrient solution containing just 5 ppm KH_2PO_4. By growing three or four seedlings per cell, a robust root ball ideal for transplanting resulted after 4 weeks at 20°C following 1 week at 25°C in the dark for germination.

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6

Agronomy and Crop Production

The production and agronomy of onions was reviewed by Brewster (1990b) and Bosch-Serra and Currah (2002), and tropical onion production by Currah and Proctor (1990). Leek production was reviewed by de Clercq and van Bockstaele (2002), and shallot production by Rabinowitch and Kamenetsky (2002) and Messiaen *et al.* (1993); the latter authors also describe garlic production in some depth. This chapter draws on these sources, and more detailed bibliographies can be found in the above reviews.

ONION PRODUCTION

Type of crop

Onions are grown for a variety of purposes, namely as fresh shoots for green 'salad' onions and as bulbs for: (i) consumption uncooked; (ii) consumption cooked; (iii) pickling; (iv) use in factory-made food; (v) dehydration; (vi) seed production; and (vii) sets. Particular varieties have been developed for most of these purposes; for example, cultivars for dehydration have higher bulb dry matter (17–20%) than the typical 10–12%. Bulbs for consumption uncooked are frequently sweet, mild-flavoured and large, with single centres suitable for making onion 'rings'. A particular type for pickling is the small, white-skinned 'silverskin'. Special cultivars are usually used for salad production and for sets. On the other hand, bulbs for the pickling, cooked consumption, the large 'jumbo' bulb market and for use in food manufacturing could be the small, medium, large and damaged grades, respectively, from a crop of the same cultivar. Normally though, bulb production is targeted at one of these outlets by controlling bulb size by varying the plant density of the crop.

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Soil and fertilizer requirements

Onion crops can be successfully produced on most fertile soils. Soil pH in the range 6–7 is usually recommended, but on organic soils a lower pH is satisfactory; for example, in Ontario, Canada onion crops grow satisfactorily on peat (muck) soils with a pH of 4. Soils with large stones or clay clods make mechanical harvesting difficult. The soil must be sufficiently well structured to permit the preparation of a fine seedbed suitable for a small-seeded crop. Onion yields are severely reduced by soil salinity, and they are among the most sensitive crops in this respect (Allen *et al.*, 1998). Therefore saline soils are not suitable. Onion crops are grown satisfactorily on sand, silt and peat soils in the UK, and also on well-structured clays in The Netherlands.

Before sowing, the soil must be prepared. Normally, fertilizer and pre-emergence herbicides will be incorporated. Phosphate (P) and potassium (K) fertilizers, which are strongly adsorbed and held against leaching by soil solids, can be incorporated long before sowing, when the land is first ploughed. Amounts of P and K recommended in the UK range from 26–129 kg/ha of P and from 50–250 kg/ha of K, depending on the pre-existing P and K levels in the soil. Recommendations for other countries are similar, and generally emphasize the importance of soil analysis for P and K in deciding the appropriate amount to apply.

Fundamentals of nutrition

In gardening tradition onions are regarded as 'gross feeders', needing a highly fertile soil to attain maximum yields. This was corroborated by comparative fertilizer trials on 22 temperate vegetables species where bulb onions and leeks, respectively, ranked fourth and fifth most responsive to P (Greenwood *et al.*, 1980b), fourth and ninth to K (Greenwood *et al.*, 1980a) and eighth and seventh to nitrogen (N) (Greenwood *et al.*, 1980c). At first sight this is somewhat paradoxical, because they are among the slower-growing vegetable species, and bulb onions remove less P and K from the soil at harvest than many other vegetables that achieve maximum yields with lower soil levels of P and K, e.g. cabbages. However, because of the low root densities and lack of root hairs of alliums (see Chapter 2), they need a high concentration of P and K in the soil solution to drive diffusion to the root surface at a rate sufficient to satisfy their requirements as seedlings.

Figure 6.1 shows the phosphorus inflow per unit root length of young onion seedlings soon after emergence. At the earliest date in Fig. 6.1, the inflow rate is nearly threefold that of later on. Hence a high soil solution concentration is needed to meet nutrient requirements for maximum growth rates of seedlings, but later inflows can be sustained by lower concentrations. The need for high soil fertility is probably largely a reflection of this short but crucial stage in crop development. Onions and other vegetable crops restricted by shortage of nutrients at this early stage are likely to remain lower yielding than unrestricted crops until final harvest (Costigan *et al.*, 1983).

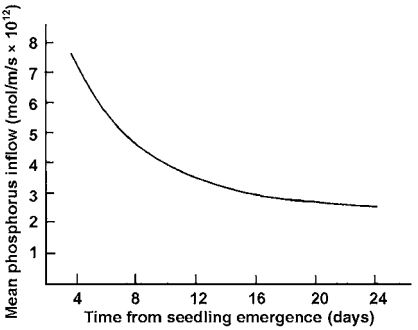

Fig. 6.1. The mean phosphorus (phosphate) inflow (uptake per unit length) into the roots of onion seedlings during the early stages of growth in near-optimal conditions in a soil of moderate P status (soil C of Brewster *et al.* (1975) with solution phosphate concentration 0.0325 mol/m^3).

The pattern of total nutrient uptake of a bulb onion crop is shown in Fig. 6.2b. It is clear from Fig. 6.2b that around 70% of N and P uptake and growth in dry weight occurred during the final half of the overall growth period. In Swedish conditions, about 80% of N uptake took place in the final third of the growth period (see Fig. 6.4). To achieve high yield it is essential to supply sufficient N to satisfy the high demand at this stage when bulbs are bulking-up.

Figure 6.2c shows a decline in the percentage of mineral nutrients in an onion crop dry matter with time. The percentage mineral nutrient content of most crops declines as crop weight per unit area increases. This can be explained by the concentrations of N, P and K being higher in metabolically active tissue than in structural and storage tissue. A certain minimum concentration (percentage of a dry weight) of a mineral nutrient occurs in live, non-growing plants. Above this minimum, relative growth rate (RGR) increases with percentage nutrient in the dry matter up to a critical percentage that can be seven- or eightfold the minimum level, provided other nutrients are non-limiting (Agren, 1988).

Relative growth rate increases linearly with percentage N in this range and quadratically with percentage P (Agren, 2004). As crop mass per unit area increases, the proportion of non-growing structural and storage tissues increases, and therefore RGR declines and the concentrations of nutrients per unit of total dry weight required to keep growth rates near maximal (termed the 'critical nutrient concentrations') decline (Greenwood *et al.*, 1991). The relationship between the critical percentage N and crop weight per unit area found in N fertilizer trials with onions was fairly well described by an equation common to many C_3 plants (see Fig. 6.3a), although at low weights the data for onion fall below this line, possibly because it has an inherently low RGR and therefore a lower critical N requirement than faster-growing crops.

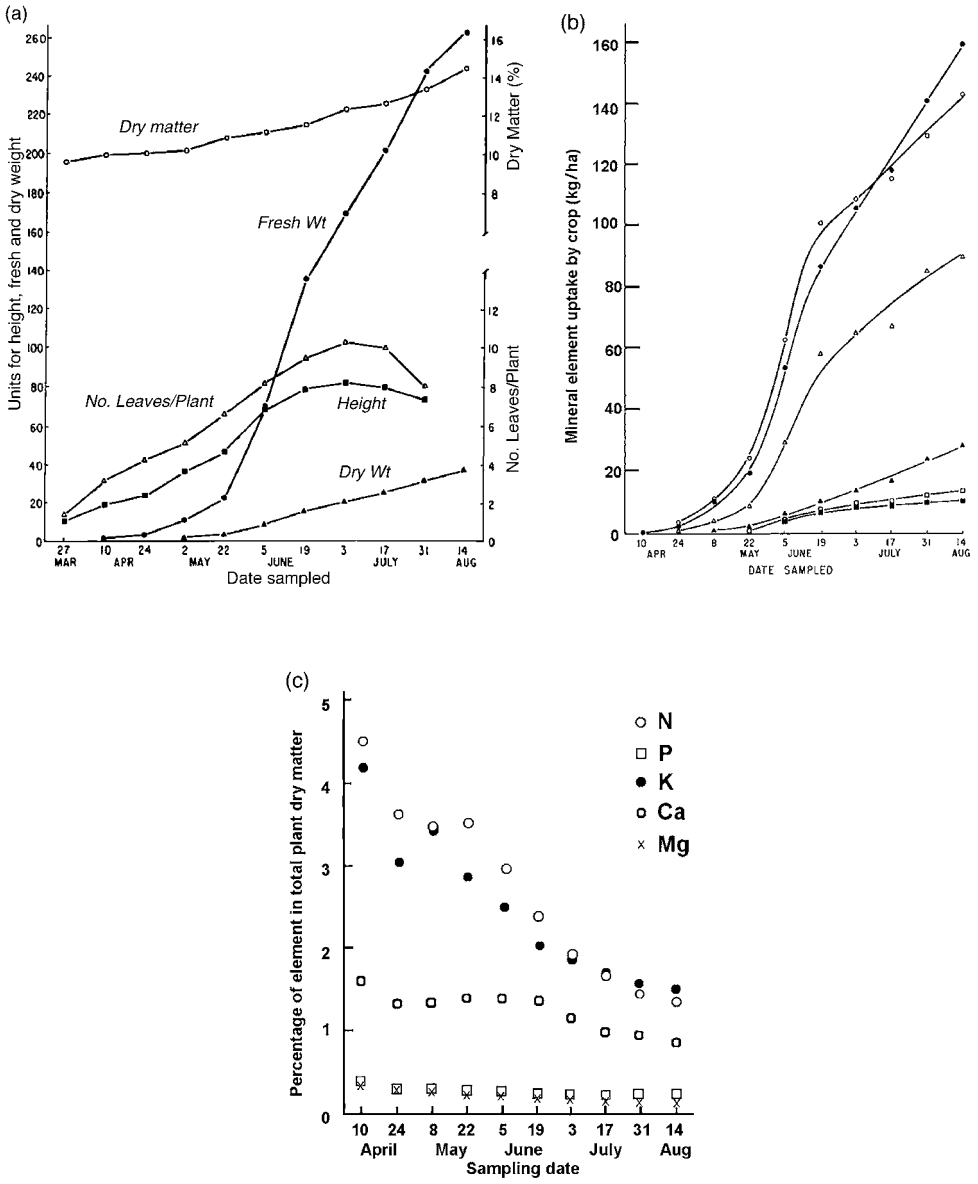

Fig. 6.2. Growth and mineral nutrient uptake by a bulb crop of onion cv. 'Southport White Globe' growing in the Salinas Valley of California, USA. (a) Growth in whole plant, fresh and dry weight (including roots, g), dry matter (%), height (cm) and leaf number. (b) The uptake of major mineral nutrients by the crop. ●, N; ○, K; △, Ca; ▲, P; □, Mg; ■, Na. (c) The concentration (%) of the major mineral nutrients in total plant dry matter during crop growth (from Zink, 1966. Courtesy of *Hilgardia*).

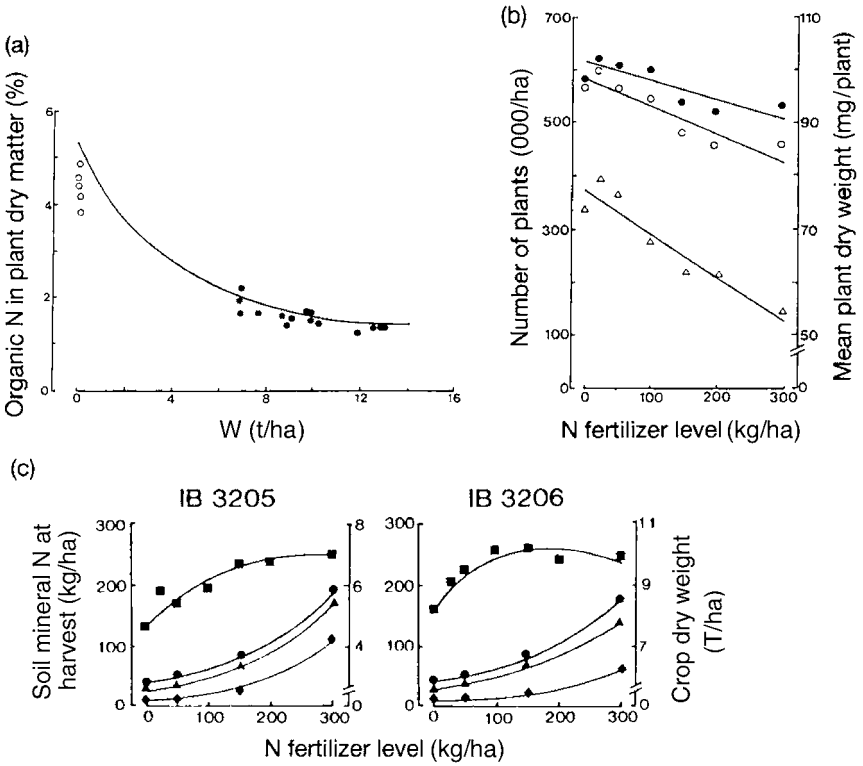

Fig. 6.3. (a) Relationship between organic N (%) and weight per unit area in dry matter of onions that were not growth limited by N, as young plants in June (○) and as bulbs in September (●). The line is the expected relationship for a C_3 species. (b) Effects of fertilizer N on plant population in June (○) and at final harvest in September (●), and on mean plant dry weight in June (△) on a light loam soil. (c) Effect of fertilizer N on onion dry weight yield per unit area (■) and on mineral N in the depth ranges (cm) 0–90 (●), 0–60 (▲) and 0–30 (♦) for a September harvest of ripe bulbs on two light loam soils in The Netherlands (right-hand graph is from the same soil as for graph (b)) (from Greenwood *et al.*, 1992. Courtesy of *Fertilizer Research*).

The critical K concentration behaves similarly to critical N, and the ratio of critical percentage K:critical percentage N is 0.595 for onion and 0.902 for leeks (Greenwood and Stone, 1998). The critical percentage P is roughly eight- to tenfold lower than the critical percentage N, and also declines as crop weight increases (Greenwood *et al.*, 1980d).

The bulb onion crop presents a considerable challenge to supply nutrient uptake per unit root length at a sufficiently high rate to permit the maximum RGR of seedlings and, later, during the main period of bulb growth to supply sufficient total N from their restricted rooting depth to achieve maximum bulb

yields. Various nutrient application techniques have been developed to satisfy the requirement for a high inflow per unit root length of young seedlings and a high total demand during bulbing, while trying to minimize nutrient losses and consequent pollution.

Simulation models for the responses of many crops, including onions, to N, P and K fertilizer have been developed (Greenwood *et al.*, 1996, 2001; Greenwood and Karpinets, 1997). These models use weather data to simulate crop growth, nutrient uptake, water uptake and losses and gains of nutrients from different depths of soil and give a prediction of nutrient responses with different climatic conditions and applications of fertilizer. They incorporate the numerous interacting processes influencing crop response to nutrients. As well as indicating appropriate fertilizer applications, they are useful for studying how different conditions may influence nutrient responses. The models are accessible on the internet (http://www.qpais.co.uk).

Nitrogen fertilizing

When it comes to nitrogen fertilizer requirements, onions present one of the most difficult crops to satisfy in an efficient fashion. To attain maximum bulb yields, rates of fertilizer must be applied that result in considerable residual N being left in the soil at harvest. Typically, yields increase with increases in N application in the range 0–150 kg/ha, and thereafter level off. However, even in the range where yield is increasing sharply with additional N, the quantity of N remaining in the soil after harvest increases (see Fig. 6.3c).

Consequently, the recovery of applied N by the crop decreases as application increases, and is typically only about 37% at the application rates needed for near maximum yields. This poor capacity to exploit soil N is again probably a consequence of the shallow, sparse root system. As a further complexity, onions are among the most sensitive crops to soil salinity, particularly at seedling emergence, and both plant population and initial plant size are lowered by initial nitrate applications sufficient to achieve maximum final yield (see Fig. 6.3b), the degree of population reduction being related to the nitrate concentration in the soil.

To overcome this difficulty it is necessary to split N applications, typically applying 60–80 kg/ha mixed into the soil as a base application just before sowing, and a similar amount broadcast when the plants are about 10 cm tall. The total quantity of N applied should be adjusted to account for the nitrate already present in the soil before fertilizing. This can be determined by soil analysis, and derives from nitrate left from fertilizing the previous crop and the mineralization of organic matter. For spring-sown bulb onion crops in The Netherlands it is recommended that total available N in the top 60 cm of soil from both added fertilizer and pre-existing sources should equal 180 kg/ha.

In Germany and Scandinavia (Stone, 2000b; Gertsson and Bjorklund, 2002) target values for mineral N content in the top 30 cm of soil at successive stages of onion crop development have been determined. These target values

must be sufficient to supply a crop with the expected total yield and N uptake. For example, in southern Sweden, bulb yields of 60 t/ha absorbing 120 kg/ha are aimed for (Gertsson and Bjorklund, 2002). The amount of mineral N in soil is difficult to predict and varies from year to year, since rates of mineralization and leaching are affected by weather conditions. By analysing the soil as onion crops develop, the quantities of N fertilizer applied at each stage can be adjusted, so that the sum of all mineralized plus fertilizer N equals the target value at each stage (see Fig. 6.4). A simplified system involving just two target N values in the top 30 cm of soil – 40 kg/ha at sowing and 120 kg/ha when the crop mass is about 1 t/ha – is more easily manageable for growers and almost as effective. To achieve maximum potential yields using these N balance techniques a certain quantity of residual N, termed the 'N buffer', must be left in the soil after harvest (Stone, 2000b).

Environmental concerns have prompted research on rotations in which the high residual N remaining in soil after onion crops is exploited by a deeper-rooting successor crop like sugarbeet or maize. In experiments in Colorado, USA, furrow-irrigated onions recovered only 15% of up to 224 kg/ha N applied, a level typical of commercial practice. Maize, planted the following year without additional fertilizer, recovered 24% of the applied N, giving a total recovery of 39% of fertilizer N from the two-crop system (Halvorson *et al.*, 2002).

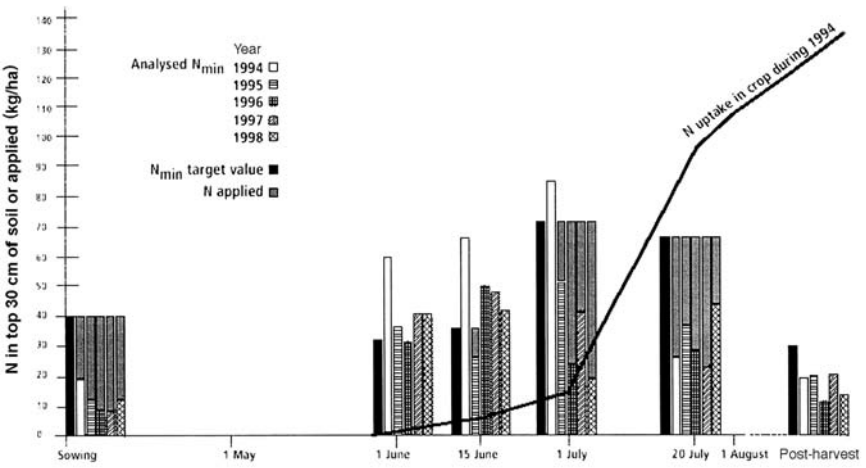

Fig. 6.4. The amounts of mineral nitrogen (N_{MIN}) found in the top 30 cm in a light soil in southern Sweden and the quantities of applied N fertilizer needed to make up the N content to this depth to target values required at sowing, 1 June, 15 June, 1 July and 20 July in five successive seasons. The target values were considered sufficient to produce bulb yields of 60 t/ha without leaving a large quantity of residual mineral N in the soil after harvest. The amounts of mineralized N varied considerably from year to year, so that the quantities of applied N needed to meet the objectives also varied from year to year (from Gertsson and Bjorklund, 2002. Courtesy of *Acta Horticulturae*).

Starter fertlizers

Improved recovery of mineral N from soil can be achieved using liquid ammonium phosphate starter fertilizer injected 25 mm below the seed at sowing time (Stone, 2000a). Using this system near-maximal yields (59 t/ha of bulbs), which required 130 kg/ha of broadcast N, were attained using only 85 kg/ha N, of which 20 kg/ha was in the starter solution and the remaining 65 kg/ha was applied and irrigated in when the crop was about 1t ha (about salad onion-size plants). The starter fertilizer gives a high P concentration just below the seedling root, and this is able to supply the high inflow needed at this stage (see Fig. 6.1), resulting in much enhanced growth, even in relatively P-rich soils (see Figs 6.5a and 6.6).

The resulting larger plants with larger root systems could extract N from the rest of the soil volume more efficiently than plants grown without starter fertilizer. Ammonium phosphate fertilizer is adsorbed on soil solids and therefore does not cause a damaging increase in soil solution concentration (salinity) below seedlings. Furthermore, experiments indicate that onions grow better when supplied with ammonium rather than N at the seedling stage (Abbes *et al.*, 1995). The accelerated early growth can result in higher bulb yields at lower N levels than with broadcast fertilizer N alone (see Fig. 6.5b). N recovery was increased by a factor at of 1.6 in the responsive range, perhaps eliminating the need for a residual 'N buffer' that remains in the soil after harvest. The faster early growth using starter fertilizer results in the earlier

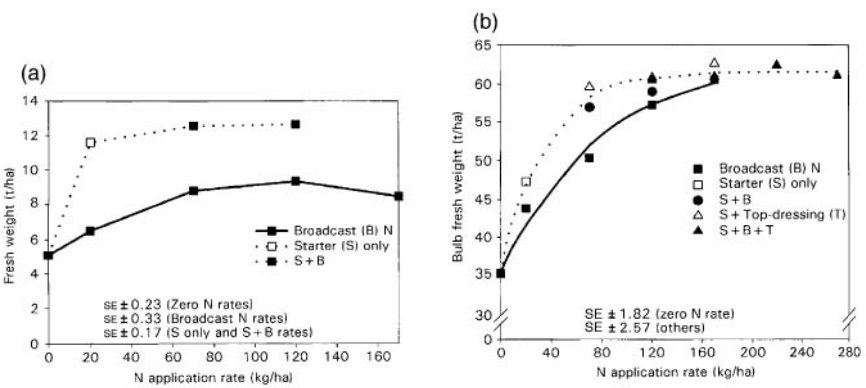

Fig. 6.5. The effects applying 20 kg/ha of N as ammonium phosphate 'starter' fertilizer below the seeds at sowing on the response of onions to broadcast ammonium nitrate mixed into the soil before sowing. (a) Green onions 9 weeks after 50% seedling emergence. (b) Yields of marketable bulbs at maturity, also showing the effects applying ammonium nitrate as a 'top-dressing' (T) and irrigating it into the soil 9 weeks after emergence, both with and without 'starter' and basal fertilizer. The levels of top-dressing tested were 50, 100 and 150 kg N/ha (from Stone, 2000b. Courtesy of *Soil Use and Management*).

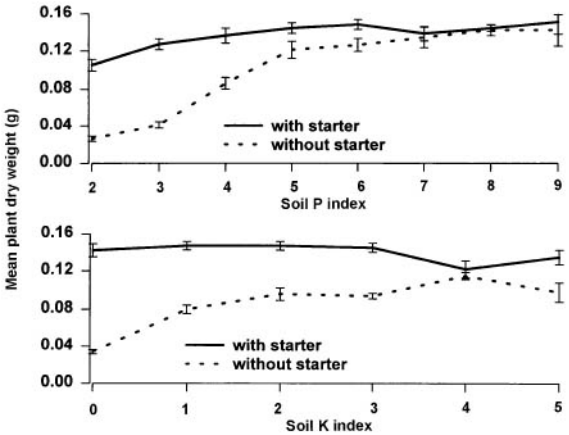

Fig. 6.6. The effects of applying liquid 'starter' fertilizer injected below seeds at sowing on the early seedling growth of onions in a sandy loam soil with a gradient of available P and of available K. The liquid fertilizer consisted of a mixture of ammonium phosphate and potassium phosphate, which delivered 375, 980 and 920 mg/m per row of N, P and K, respectively. Extraction, analysis and indexing of soil P and K levels were performed according to UK recommendations (MAFF, 2000) (from Stone, 1998. Courtesy of the *Journal of Horticultural Science and Biotechnology*).

attainment of a high Leaf Area Index (LAI), which causes earlier bulb maturity for the reasons outlined in Fig. 4.33 (Brewster *et al.*, 1992). This tends to lead to better quality at harvest and less likelihood of non-ripening, 'thick-necked' bulbs.

Starter fertilizers may enable vegetable crops, including onions, that need soils of high P and K fertility to yield well and to be grown successfully on soils of lower P and K status than previously. Maintenance applications of 100–200 kg/ha of P and K are applied annually to many soils to maintain high levels of plant-available P and K, to counteract the constant tendency for these nutrients to become fixed in unavailable forms and for the available P and K levels to stabilize at a lower steady-state concentration (Karpinets and Greenwood, 2003; Karpinets *et al.*, 2004). This is both wasteful of fertilizer and potentially polluting, particularly if soil of high P and K levels is eroded into waterways, where it can contribute to eutrophication.

Stone (1998) demonstrated that injection 25 mm below seeds of a liquid starter fertilizer of ammonium phosphate plus potassium phosphate giving 375, 980 and 920 mg of N, P and K, respectively, per m row (equivalent to 10, 27 and 25 kg/ha N, P and K, respectively) virtually eliminated any effect of soil P or K fertility on onion seedling growth (see Fig. 6.6). In a further experiment, starter fertilizer combined with injection of liquid NPK to make a total fertilizer application of half the recommended rate for onion bulbs, gave a higher yield than

basal treatments of fertilizer at the full recommended rate. The supplementary N, P and K was injected after emergence 150 mm to the side of the plants at a depth of 60 mm. Thus, starter fertilizers combined with injection of further fertilizer after emergence may make it possible to grow high-yielding onion crops at lower levels of available soil NPK than is possible using conventional broadcast fertilizer. Starter fertilizers are now widely used commercially in the UK on bulb and salad onion and leek crops.

Micronutrients

As regards other nutrients, problems due to deficiencies of certain trace elements have been periodically reported, particularly on peat (muck) soils. Copper deficiency causes twisted, chlorotic leaf tips and bulbs with pale, thin and brittle skins. Copper sulfate incorporated into the soil – or foliar sprays with 0.25% copper sulfate solutions – have corrected this problem. Ellerbrock (1997) developed guidelines for copper requirements on peat soils based on the quantity of HCl-extractable copper in the soil. Manganese deficiency, which causes stunting and a striped chlorosis of outer leaves, occurs on peat soils of pH > 6.5 and on chalky-clay soils high in phosphate. The problem can be cured by foliar sprays applying 15 kg/ha of manganese sulfate or by soil application of larger amounts. Zinc deficiency, curable by foliar sprays of zinc sulfate, and molybdenum deficiency, curable by molybdenum seedcoatings, have been reported on high- and low-pH peat soils, respectively.

Mineral nutrients and flavour

The effects of mineral nutrition on allium flavour have been reviewed by Randle and Lancaster (2002). Sulfate availability probably has the greatest effect on flavour intensity and quality of any environmental factor. Limiting sulfur or making it abundant to the plant inevitably impacts on the quantity of sulfur-based flavour-precursor compounds synthesized (see Chapter 8). Freeman and Mossadeghi (1970, 1971) first showed that flavour intensity could be varied from almost negligible levels to high levels by varying the sulfate supply to onion and garlic plants growing in nutrient solutions. Their work showed that a saturation point was reached, after which additional sulfate resulted in little increase in pungency. However, in field experiments, pungency has rarely responded to applied sulfur (Hamilton *et al.*, 1998), since the element is already adequately supplied in most soils and sulfate is often added through normal fertilizer practices.

For many types of onion high flavour intensity is desired. However, for the production of very mild onions, the restriction of sulfate to the plant is necessary. To produce mild onions, sulfate in the soil and water should not be above 50 ppm (Randle and Lancaster, 2002). Sulfate is a readily leachable anion, like nitrate, and is more easily leached from light, sandy soils than heavy or highly organic soils, and hence light soils are most suitable for mild onion production. Since sulfur is an essential element for normal plant growth,

restricting sulfate to produce mild onions can result in lowered bulb yields (Randle and Lancaster, 2002).

Sulfate fertility also affects sugar and soluble solids accumulation in onions. Cultivars with the potential for mild flavour increase sugar content with low sulfate, whereas some other cultivars decrease their solids and sugars (Randle and Bussard, 1993). Some onion cultivars are greatly affected by changes in available sulfate while others show less response. When onions are grown under high-sulfate fertility, more sulfur is retained in the leaves during bulbing than at low sulfate. If leaves are allowed to senesce and dry on the bulbs, very little sulfur remains in the leaves of plants grown under low-sulfate fertility. As sulfate fertility increased, the amount of total bulb sulfur stored as sulfate increased from approximately 10 to almost 50% (Randle *et al.*, 1999).

Pungent cultivars accumulate a lower percentage of sulfate in the bulb compared with mild cultivars. Pungent cultivars have a greater metabolic requirement for sulfur and more efficiently incorporate sulfur into the pathway, leading to flavour precursors, whereas mild cultivars can partition a greater proportion of absorbed sulfur to sulfate, thereby excluding it from the ACSO pathway (see Chapter 8).

Sulfur fertility affects how organic sulfur accumulates and the latter is metabolized through the various peptides and precursors of the flavour pathway. Under high-fertility conditions, 1-propenyl cysteine sulfoxide accumulates in the highest concentrations. As sulfur fertility decreases to near deficiency levels, methyl cysteine sulfoxide increases in concentration and becomes the dominant precursor (Randle *et al.*, 1995). Propyl cysteine sulfoxide, which is normally the lowest-concentration precursor, was found in higher concentration than 1-propenyl cysteine sulfoxide when S fertility approached deficiency levels. At these levels, 95% of all sulfur in the bulb occurred as flavour pathway compounds whereas, at high-sulfur fertility, less than 40% of bulb sulfur was in such compounds.

Selenate, which is chemically analogous to sulfate and competes with it in root uptake and biochemical reactions, can cause a decrease in pungency in onions. Supplying sodium selenate to roots had a similar effect on flavour quality to low-sulfur fertility levels, namely methyl cysteine sulfoxide content increased and 1-propenyl cysteine sulfoxide levels decreased (Kopsell and Randle, 1999). Chloride, an essential element for onions because it is the counter-ion to potassium in regulating stomatal turgidity, is also a competitor with sulfate in absorption by roots. Onions supplied with high calcium chloride had decreased pungency and lower sulfur accumulation in bulbs (Randle, 2005).

Plant density, row spacing and the control of bulb size

From the physiology described in Chapter 4, it is clear that cultivars must be well adapted to the photoperiods and temperatures of the locality and growing

season. If this is the case, the size of bulbs can be controlled to a considerable extent by the planting density (see Fig. 6.7). For example, the small bulbs (sets) used for planting in the following year are grown at a density of 1000–2000 plants/m^2, whereas 5–7 cm diameter bulbs for cooking must be grown at 50–100 plants/m^2. To produce larger 'jumbo' bulbs, planting densities of 25–50 plants/m^2 are used. Onion bulb yields increase to an asymptote as plant density increases, and mean bulb size correspondingly declines (see Fig. 6.8).

The maximum yield attained at high density depends on growing conditions, particularly soil fertility and water availability. The highest yields attained in fertilized irrigated plots or under fertigation are about 100–120 t/ha (about 10 t/ha of dry matter). Good commercial yields are about half this amount. In drier, poorer, less fertile parts of the world yields are much lower on average. It follows that the yield:density relationship depends on fertility and, therefore, so does the spacing needed to produce a particular mean bulb weight. If the crop yield can be forecast, Eqn 6.1 can be used to specify the plant density needed to produce bulbs of the required weight:

$$(\text{Bulb Weight})^{-1} = A + B \times (\text{Plant Density}) \qquad \text{(Eqn 6.1)}$$

A and B are fitted parameters, where 1/A corresponds to the maximum bulb size attainable at very low densities and 1/B corresponds to the maximum or asymptotic yield attained at high densities. The value of 1/B measures the 'yield potential' of the environment. Equation 6.2 can be used to estimate diameter from weight (Rogers, 1978):

$$\log_{10}(\text{bulb diameter(mm)}) = 1.02 + 0.364\log_{10}(\text{fresh wt(g)}) \qquad \text{(Eqn 6.2)}$$

Equation 6.2 is slightly inaccurate because the length:diameter ratio of bulbs tends to increase as plant density increases.

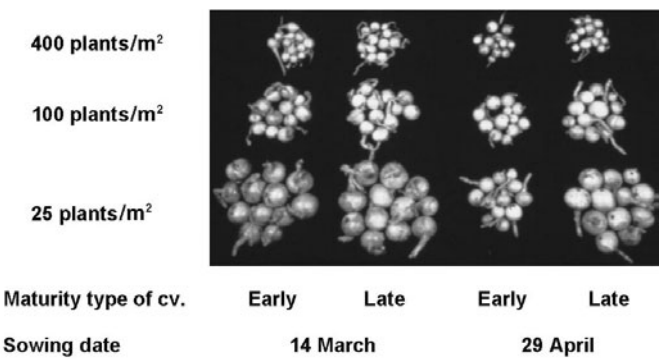

Fig. 6.7. The effects of plant density, sowing date and cultivar on the bulb size at harvest of spring-sown onions (photograph courtesy of Warwick HRI, UK).

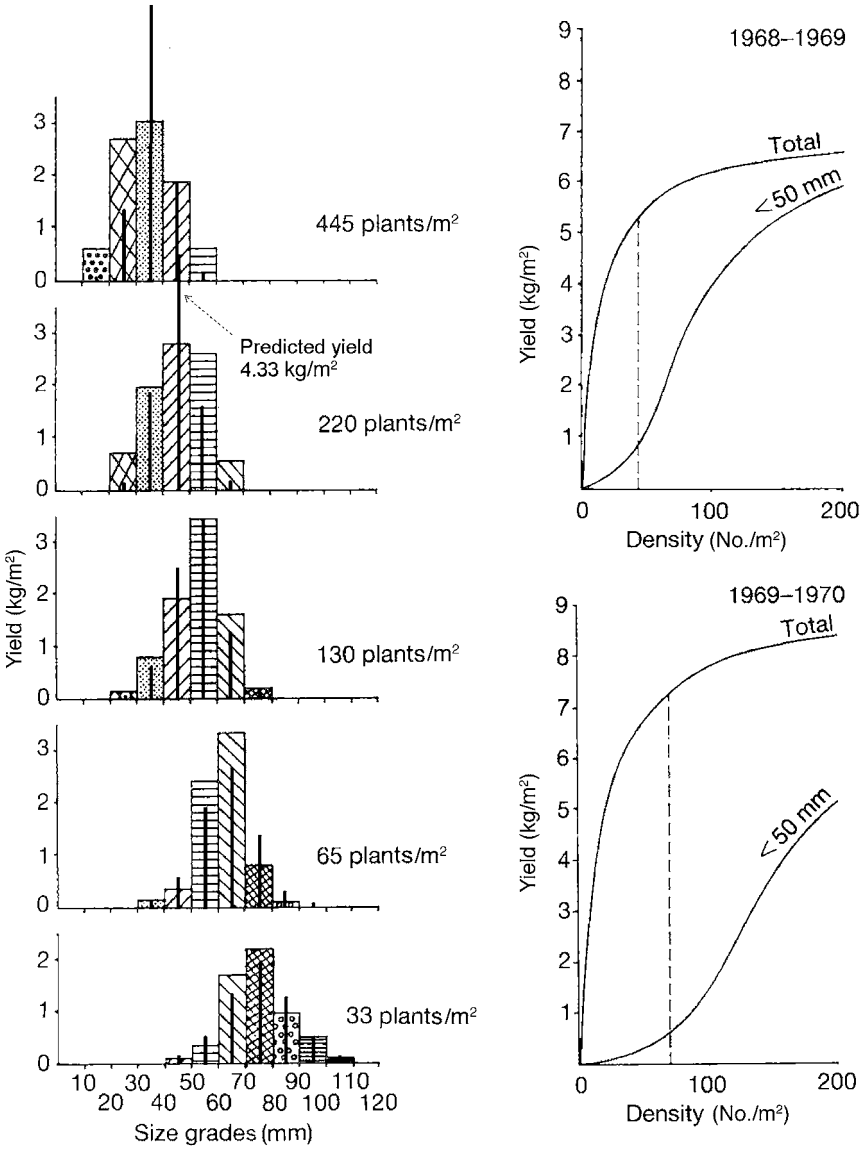

Fig. 6.8. The effect of plant density on the yield of bulb onions in varying diameter grades in 1970, and on yields of total and bulbs < 50 mm diameter in two seasons in New Zealand that differed in maximum yield attained. The vertical lines within each histogram bar show the predicted weights of bulbs within each size class, as calculated using Eqn 6.1, with values of A and B given for 1970, and Eqn 6.3 (from Frappell, 1973. Courtesy of the *Journal of Horticultural Science and Biotechnology*).

Beyond simply mean bulb weight and diameter, as predicted by Eqns 6.1 and 6.2, equations have been derived to predict the distribution of bulb yield over different weights and diameters (de Visser and van den Berg, 1998). Thus:

$$F(w) = 1/(1 + e^{((m-d)/b)}) \quad \text{(Eqn 6.3)}$$

F(w) = the proportion of the total bulb weight with a diameter less than or equal to d

d = bulb diameter, mm

m = the diameter of a bulb at the mean weight (i.e. where F(w) = 0.5)

b = a constant that varies with the diameter of a bulb at the mean weight (b = 0.0991m)

m is related to the cube root of the mean bulb weight and can be found using the equation: $m = 13.2\ w_m^{1/3}$, where m is in mm and w_m is the mean bulb weight, g.

Equation 6.3 was developed in The Netherlands using data from plots with plant densities ranging from 52 to 185 plants/m^2 of the fairly spherical 'Rijnsburger' type onions. Predicted size distributions from Eqn 6.3 along with Eqn 6.1, using the values for A and B for 1970 given by Frappell (1973), are compared with those observed for cv. 'Pukekohe Long Keeper' in New Zealand in Fig. 6.8. At densities between 33 and 130 plants/m^2, i.e. in the range typical for bulb onions, the predictions are good despite the difference in location and cultivar. Thus, if a target mean yield can be achieved, the weight and number of bulbs in each grade can be predicted.

Trials comparing various row widths with the same overall plant density have consistently shown increases in yields as row widths decrease. For example, in moving from rectangularities (inter-row distance/mean within-row distance between plants) of 8 to 1, increases in bulb yield of 10–20% have been reported. Inter-row spacings of 45–60 cm, necessary for inter-row cultivation before herbicidal weed control was well established, do not give maximum yields of bulb onions. Herbicides have enabled growers to adopt the 'bed' system of vegetable growing and to use plant spacing arrangements that enable crops to fully exploit light and soil resources and give high yields.

Planting density and shallot size

Similar principles apply to the control of bulb size in shallots (Cohat, 1986; Messiaen *et al.*, 1993). The size of bulbs harvested depends on the number of daughter bulbs formed per unit area, and this can be varied by two factors: the number of mother bulbs planted per unit area and/or their size. The growing points giving rise to daughter bulbs are already present in a mother bulb when it matures, and cannot be modified by storage conditions, planting date or density. The number of daughter bulbs produced per mother bulb planted depends primarily on the weight of the mother bulb. For bulbs raised under similar conditions, Eqn 6.4 gives the relation between bulb weight, w and the number, n of buds within where k_1 is a constant:

$$n = k_1 \sqrt{w} \qquad \text{(Eqn 6.4)}$$

Hence, planting large mother bulbs at a high planting density results in a high density of daughter bulbs of small size, whereas planting small mother bulbs at low density results in a low density of daughter bulbs of large size. Table 6.1 shows the distribution of daughter bulbs that resulted from the extreme treatments in a French trial. The same size distribution of harvested bulbs can result from different combinations of mother bulb size and planting density, so long as they result in equal numbers of daughter bulbs. It can be seen from Table 6.1 that treatments gave a threefold difference in the number of daughter bulbs, but yield increased by a factor of only 1.3, so mean bulb size was much reduced from the heavier planting weight.

Although the number of daughter bulbs originating from a mother bulb depends primarily on its weight, the level of competition experienced by the mother bulb when it grew has some additional influence. In experiments in which cv. 'Jersey demi-longue' mother bulbs of equal size were selected from bulbs produced from densities at planting ranging from 14 to 29/m^2 using bulbs weighing 10, 15 or 20g, the lower the degree of competition the mother bulbs were subject to the greater the number of daughter bulbs produced. A mean of 5.9 daughter bulbs was produced by 10 g bulbs and 8.3 by 20 g bulbs; but 10 g bulbs themselves produced from 10 g bulbs at 14 plants/m^2, i.e. under the lowest competition gave rise to seven daughter bulbs, whereas those raised from 20 g bulbs at 29 plants/m^2, i.e. under the highest competition, gave rise to 5.2 daughter bulbs. The corresponding extremes for 20 g bulbs were 10.4 and 7.3 daughter bulbs.

The relation between the yield, Y of shallots and the number of buds (i.e. daughter bulbs) per ha (N), with k_2 as a fitted constant, is of the form:

$$Y = k_2 N^{1/3} \qquad \text{(Eqn 6.5)}$$

Equations 6.4 and 6.5 were derived for spring-planted 'Jersey demi-longue' shallots grown in western and central France and also apply to tropical shallots grown in the West Indies. Grey shallots (see Chapter 1) and autumn-planted shallots do not conform to these equations (Messiaen *et al.*, 1993).

Dates of sowing

In many regions sowing dates are limited by the climate to a short period in the spring or in the autumn of the year. In many mid-latitude regions – for example, Israel – sowings can be made throughout the autumn, winter and spring to give a succession of harvest dates. Autumn sowing is common in low and intermediate latitude regions with mild winter temperatures which permit some crop growth. Onions can survive temperatures of –6°C but are killed by temperatures of –8 to

Table 6.1. Weight distribution of shallot bulbs in varying diameter grades at harvest that resulted from combinations of mother bulb weight and planting density giving low and high intensities of inter-shoot competition (from Cohat, 1986).

Mother bulb weight (W, g)	Plants/m^2 (D)	Weight planted (W × D, t/ha)	Number harvested/m^2	Number harvested per clump	13–19 mm (t/ha)	19–25 mm (t/ha)	25–28 mm (t/ha)	28–32 mm (t/ha)	> 32 mm (t/ha)	Total yield (t/ha)
10	14	1.4	100	7.1	0.1	1.5	3.1	5.1	15.3	25.1
20	29	5.8	330	11.4	7.9	19.1	4.6	1.0	0.2	32.8

–11°C, with younger, smaller seedlings being killed at the higher end of this range. Overwinter growth is typical of regions famous for their 'early season' production of bulb onions – for example, the Rio Grande valley of Texas, USA.

At higher latitudes, longer, colder winters make autumn sowing impracticable except in maritime areas, and the crop must be grown from spring sowing or planting. The higher the latitude the shorter the growing season and, ultimately, there may be insufficient length of season for the small-seeded, rather slow-growing onion crop to make an adequate leaf area and to bulb before the end of the growing season. In such regions bulb onions may be grown from transplants sown in glasshouses in the late winter, thereby extending the growing season, or they may be grown from sets produced in the previous year. By using a set with a dry weight of about 0.2 g, rather than a seed with a dry weight of 0.003 g, the size of the plant at emergence is correspondingly greater, and the time required after emergence to make sufficient leaf area to produce a large bulb is shortened.

The timing of the late summer or autumn sowing can be critical. In the UK, sowings in early August will produce many bolters, whereas sowing after early September produces plants that are too small to survive the winter (see Fig. 6.9). The same principle can be seen in New Mexico, USA except that, at this lower

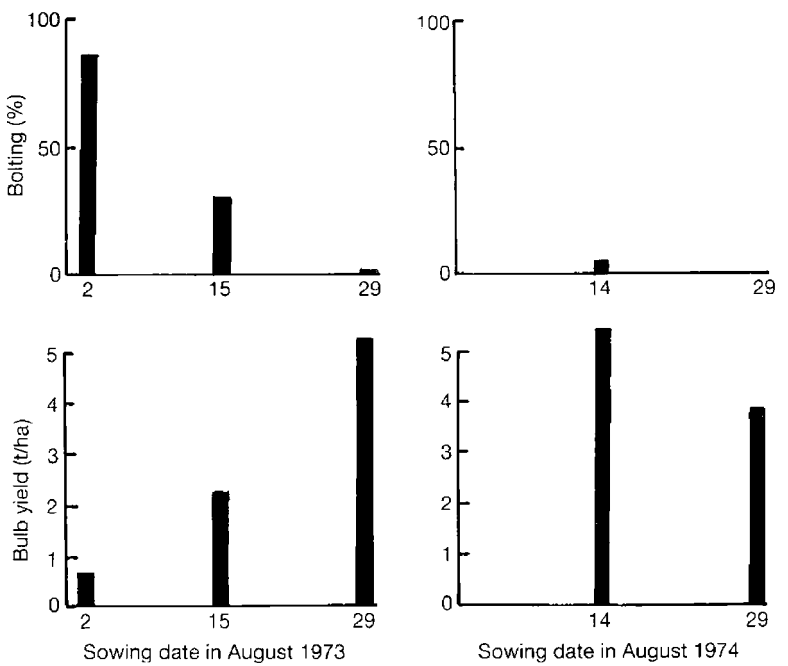

Fig. 6.9. Percentages of plants bolting and bulb yields of onion cv. 'Senshyu Semi-globe Yellow' grown from a succession of August sowings in a year with a warm autumn (1973) and in a year with a cool autumn (1974) at Wellesbourne, UK.

latitude, the relevant range of sowing dates is later: (i) early September, giving a high level of bolting and low yields; (ii) mid- to late September, giving little bolting and maximum yields; with (iii) mid-October giving no bolting but lower yields (Corgan and Kedar, 1990).

The optimum sowing date varies somewhat from year to year. In the UK, if the late summer and autumn are warm, growth may be rapid and the plants may reach the critical size needed to induce flowers (see Chapter 4) by late autumn from a mid-August sowing, as in 1973 (see Fig. 6.9). Consequently, such plants will be fully vernalized during the winter and a high percentage will bolt. In a season with a cool autumn, like 1974 (see Fig. 6.9), this will not occur, since plants sown in mid-August will not reach the critical size needed for vernalization to begin until the spring.

Because it is critical that autumn-sown crops reach a size sufficient to withstand the winter, it is essential to provide seedbed irrigation as well as the correct sowing date. Seed sown into dry soil will not germinate until moistened and, without irrigation, the start of growth will therefore depend on the vagaries of rainfall. Figure 6.10 shows various stages in the growth of a typical overwintered bulb onion crop grown in four-row beds.

The dates for spring sowings are limited, for different reasons. There is no point in sowing until soil temperatures have warmed sufficiently to permit germination and emergence. However, if sowing is left too late, the crop will not reach sufficient size for bulbing to be completed before temperatures and day-lengths decline in late summer sufficiently to cause bulbing to revert to leaf blade growth, thereby producing 'thick-necked' plants (see Fig. 6.11).

In The Netherlands, experience has shown there is little point in sowing onions before early April; in the UK, sowings are best done in late March. Once onion seeds have germinated they begin to lose viability if exposed to longer than 2 days at temperatures $< -2°C$ (Gray and Steckel, 1983). The probability of such damaging temperatures occurring declines as the season progresses and, at Wellesbourne, UK, it is only three per 100 sowings made in April, whereas in February it is 13 per 100. Even if seeds are not killed directly by low temperatures, the lower the temperature the slower the emergence rate and the longer time the seedbed has to deteriorate before seedlings emerge. In particular, a hard 'cap' or crust may develop, which is impenetrable to onion seedlings. Therefore both direct and indirect effects of low temperature can reduce the percentage emergence and make sowing too early in the spring a mistake.

Method of planting: direct sowing, transplanting or sets

Direct sowing

Sowing seeds directly into the soil where the crop is to be grown is potentially the most economical method of raising an onion crop, particularly where the availability of labour for transplanting is limited, its cost is high or where the

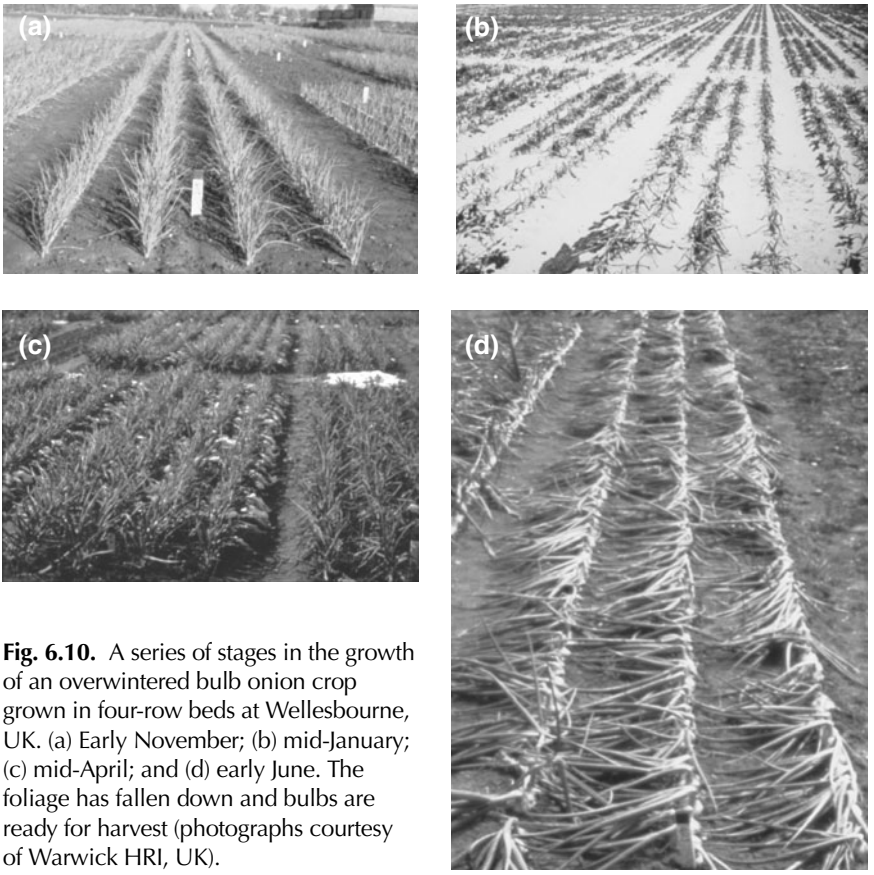

Fig. 6.10. A series of stages in the growth of an overwintered bulb onion crop grown in four-row beds at Wellesbourne, UK. (a) Early November; (b) mid-January; (c) mid-April; and (d) early June. The foliage has fallen down and bulbs are ready for harvest (photographs courtesy of Warwick HRI, UK).

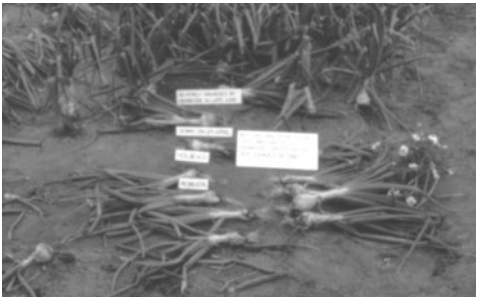

Fig. 6.11. Thick-necked onions in the autumn. Late-sown (29 April) maincrop cv. 'Robusta', damaged by herbicide in late June, fails to produce ripe bulbs by mid-September in Lincolnshire, UK. Note the elongated thick necks on plants that have partially bulbed and the plant-to-plant variation in the degree of bulbing (photograph courtesy of Warwick HRI, UK).

availability of facilities for raising transplants is limited. However, in common with many other vegetable crops having small seeds and delicate seedlings, a high standard of husbandry is required to produce a satisfactory crop from direct sowing. As discussed in detail in Chapter 4, onion seeds are slow to germinate and emerge after sowing, and these rates depend on temperature and moisture.

For effective herbicidal weed control, emergence must be spread over a short period (see Chapter 5). This requires uniform seedbed conditions as defined by temperature, moisture availability and aeration; a uniform depth of sowing, since the time to emergence will increase with sowing depth; and high-quality seed with an innate capacity for rapid germination over a short spread of time. The timing of rainfall or irrigation can strongly affect the percentage and spread of emergence (see Fig. 4.13). Irrigation is best applied when sufficient day-degrees have accumulated since sowing for most seeds to have reached the stage immediately prior to radicle emergence (approximately 90 day-degrees > 1.4°C for onions) (Finch-Savage, 1990; Fig. 4.14). Irrigation is usually essential for autumn or late summer sowing but, in many regions, spring sowings rely on rainfall and existing soil moisture.

The importance of plant density in controlling bulb size has been described above. Therefore, a predictable and high percentage of emergence, spread uniformly over the field, is important in ensuring that bulbs develop to the right size. Clearly, if the percentage emergence is spatially variable, plant density, and hence the ultimate size of bulbs, will be variable. Furthermore, plant density influences the maturity date of bulbs, with high densities reaching maturity and being ready for harvest before low densities (see Chapter 4). Therefore, a spatially variable percentage emergence will create difficulties in determining the optimum time for harvesting, and in the timing of pre-harvest sprays of maleic hydrazide (see Chapter 7). For all these reasons, spatially uniform emergence with little spread in time is crucial for a successful onion crop.

Directly sown onion crops are normally drilled at a depth of about 2 cm. The seeds are commonly drilled in rows about 30 cm apart on to beds six rows wide. The quantity of seed required for sowing can be estimated using Eqn 6.6:

$$\text{Seeds (kg/ha)} = 1000 \times \text{Target (plants/m}^2\text{)/[seeds/g} \times \text{\% laboratory germination} \times \text{field factor]} \qquad \text{(Eqn 6.6)}$$

There are usually 300–400 onion seeds/g and, with good-quality commercial seed, the laboratory germination should exceed 90%. The 'field factor' depends on seedbed conditions: for ideal conditions this is 0.9, i.e. 90% of the viable seeds emerge; for average conditions 0.7 and, for a cold soil with poor tilth, 0.5 (MAFF/ADAS, 1982). Various types of seed drill are suitable, and precision drills that place seeds in the soil at regular intervals are widely used. Trials comparing bulb onion crops carefully thinned to a uniform within-row spacing with crops, in which the distance between plants within the row varied randomly, showed no improvement in yield or uniformity of bulb size from a uniform within-row spacing; both spacing arrangements had the same overall

plant density. Therefore, the benefits of extreme precision of within-row spacing for bulb onions are questionable.

Improved emergence and a shorter time-spread of emergence, leading to higher yields and more uniform sized bulbs, have been obtained using a 'dibber' drill rather than a conventional seed drill (Gray *et al.*, 1995). The dibber drill pushes seed into the soil while it is held by suction on the end of metal 'fingers'. It ensures a uniform depth of sowing, irrespective of corrugations in the soil surface, and good contact between seed and soil. Moreover, sown seeds can be covered with granules of wettable polacrylamide that forms a gel above the seeds, and this has been found to improve emergence.

It is 'lore' among growers and gardeners that onions require a firm seedbed. Dutch advice recommends preparing the seedbed so that the seed is sown on to a moist, firm underlying layer. Trials have shown that by preparing soil beds in the autumn, and then cultivating no deeper than the 2–3 cm sowing depth before sowing in the spring, seedling emergence can be increased sixfold in a dry spring. This technique allows the seeds to be sown on to a well-settled layer of soil with good capillary conductivity for water rising to the imbibing seeds (Rowse *et al.*, 1985). Good water conductivity to the seed is probably the main benefit of a well-firmed seedbed.

After sowing, the time to emergence depends on temperature and moisture availability. In moist soil, onions reach the stage of 50% viable seedlings visible after 140 day-degrees above a base of 1.4°C (Finch-Savage, 1986). Because onion (and leek) emergence is slow compared with other crops, and because seedlings are quite small, emergence can be reduced by soil capping. The longer the time between sowing and emergence and the finer the seedbed, the greater the probability that heavy rainfall will cause a 'cap' or crust to develop that is impenetrable to the emerging seedlings. To counter this problem, 'anti-capping' soil conditioners can be sprayed on to the seedbed after sowing to stabilize the crumb structure against destruction by heavy rain. Cellulose xanthate soil conditioners have increased onion and leek emergence by 40–80% in some trials (Page,1980).

Onions are highly sensitive to salinity, particularly as seedlings (see Figs 4.11, 4.16 and 4.19). Onions are sometimes sown part-way up a sloping ridge, and irrigation water is introduced to adjacent furrows for several days. The water is drawn up past the seeds, carrying away excess solutes to deposit them, after evaporation, on a 'salt ridge' away from the seeds (Jones and Mann, 1963).

THE PRIMING OF SEEDS Seed priming is a process in which seeds are allowed to imbibe sufficient water to enable the earlier events of the germination process to occur, but not sufficient to permit radicle emergence through the seedcoat. It increases the rate and uniformity of germination after sowing and, consequently, can result in faster, more uniform field emergence from the soil (Bradford, 1986; Khan, 1992), factors essential for the precision agronomy and size uniformity needed in modern vegetable production (Finch-Savage,

2005). After priming treatments seeds can be dried and still maintain most of the benefits of priming. Dried, primed seed can be sown using normal seed drills. Onion and leek seeds have been thoroughly investigated in research and development studies on priming, and the technique is widely applied to commercial leek seeds to improve the rate and uniformity of emergence of direct-sown crops.

Two fundamental approaches to controlling seed hydration have been used in priming. First, the seeds have been suspended in a medium with a water potential below that which allows radicle emergence but that allows sufficient hydration to progress germination up to this point. Secondly, water vapour has been slowly dosed to bulks of seed to hydrate them to the same level directly. Oxygenated solutions of polyethylene glycol (PEG) of molecular weight (MW) 6000, with the PEG concentration adjusted to give an osmotic potential of –1.5 MPa, have been used in bioreactors for large-scale priming of onion and leek seeds (Bujalski *et al.*, 1989; Nienow *et al.*, 1991). Other solutes can also be used (Gray *et al.*, 1991a).

An alternative hydration medium is a granular, solid material of water content adjusted to give a water potential –1.5 MPa into which the seeds are mixed; this is termed solid matrix priming (Taylor *et al.*, 1988). Various clay and silicaceous minerals have been used as the solid material.

The second approach to hydration is more direct, in that water vapour is injected into a slowly rotating horizontal drum of seeds in order to hydrate them progressively over 24 h to a water potential suitable for priming (i.e. –1.5 MPa for leeks and onions) (Rowse, 1996); this is termed 'drum priming'. The required amount of hydration is first determined by equilibrating small quantities of seed on a semi-permeable membrane enclosing a PEG solution of osmotic potential –1.5 Mpa, and then determining the water content of the seed by oven drying. Drum priming has the advantage for large-scale application that it does not produce a large bulk of osmotic solution or solid matrix that requires disposal after use. Drum priming is now widely used for commercial priming of leek and onion seeds in Britain (Rowse *et al.*, 1999). Both osmotic and drum priming give the same advancement of seed germination and seedling emergence (Gray *et al.*, 1990a).

Primed seed has accelerated germination and a reduced spread of germination compared with natural seed (Fig. 4.8a). The differences in germination rate and its variability are most evident at suboptimal temperatures and water potentials (see Table 6.2). Finch-Savage and Steckel (1994) described experiments where primed leek seeds sown into a moist seedbed were able to emerge rapidly and uniformly irrespective of subsequent irrigation, whereas natural seed was slower and required irrigation either regularly or at the optimum time following sowing (see Fig. 4.14) for satisfactory emergence. The primed seeds were able to germinate and emerge before the soil had dried sufficiently to prevent growth.

Maximum advancement of onion and leek seeds by priming occurs when they are hydrated to a water content of about 45% of fresh weight. It takes

Table 6.2. Mean germination time[a] (GT) and its standard deviation (SD) for natural and drum-primed leek seed[b] sown under different temperatures and osmotic potentials (from Rowse, 1996, Tables 4 and 6).

		Osmotic potential (Mpa)			
		–0.1		–0.3	
Temperature (°C)	Seed	GT	SD	GT	SD
5	Natural	19.33	3.90	29.66	8.19
	Primed[c]	1.08	1.02	2.89	2.49
15	Natural	3.41	0.92	5.18	1.44
	Primed[c]	0.75	0.34	0.74	0.40

[a]Germination was tested on absorbent paper moistened with the PEG solutions.
[b]Cv. 'King Richard'.
[c]Undried primed seed.

7–14 days at 15°C at this moisture content to achieve maximum advancement for leek and onion seed. Advancement is less for seeds held at lower moisture content and was zero at 30% seed moisture content (Gray *et al.*, 1990b).

The advancement of germination that results from priming is greater for slower-germinating seedlots (Drew *et al.*, 1997). Priming can increase the percentage of normal seedlings that develop from the germinating leek seeds provided the seeds are sown soon after priming (Drew *et al.*, 1997).

Primed seeds are normally dried after treatment for ease of handling and distribution. About 1 day of the advancement gained from priming is lost while the dried, primed seed rehydrates after sowing, but most of the decrease in time to germinate and decreased spread of emergence is retained. Dried, primed seed can be stored for some time, but long-term storage – e.g. greater than 100 days at 10°C and 40% RH – resulted in an increasing percentage of abnormal leek seedlings that failed to produce roots (Maude *et al.*, 1994).

Priming simply accelerates germination of seeds – the relative growth rate after germination of seedlings from primed or unprimed seeds has been shown to be the same for both onions (Ellis, 1989) and leeks (Brocklehurst *et al.*, 1984).

The volume and the number of cells per seed embryo do not change during the priming of onion and leek seeds (Gray *et al.*, 1990b). DNA synthesis, of which approximately 20% is DNA repair-type synthesis, occurs during priming of leek seeds despite the absence of cell division (Ashraf and Bray, 1993). During priming, overall DNA levels in leek seed embryos do not increase, but RNA levels increase by 50–100% (Bray *et al.*, 1989; Clarke and James, 1991). In primed leek seeds germinated at 15°C, after an initial lag of 6–12 h, DNA, RNA and protein synthesis increases in seed embryos much faster than in unprimed seed. Furthermore, seeds having a low rate of biosynthesis compared with more 'vigorous' seed during normal germination have rates of biosynthesis equal to

vigorous seed following priming (Bray *et al.*, 1989). There is evidence, therefore, that priming allows both repair processes (i.e. DNA repair) and preparation for accelerated DNA, RNA and protein synthesis in leek seeds when they are set to germinate.

In the years 1970–1990 there was much experimentation with sowing pre-germinated onion and leek seed. Seeds were germinated in bulk in aerated water and sown with pre-emerged radicles in a gel carrier; this was termed 'fluid drilling' (Finch-Savage, 1984; Gray, 1991). Fluid drilling requires a special seed drill, whereas drum-primed seed can be sown using the conventional drills used for untreated seed. Fluid drilling also involves the transport and storage of seeds in a vulnerable germinated state and the preparation of bulky gels. The potential benefits were largely achieved using drum-primed seeds, and fluid drilling was abandoned commercially.

Transplanting

Despite the development and improvement of direct sowing, transplanting is still widely used in both temperate and tropical regions. Direct sowing will probably always be subject to a greater risk of failing to establish a uniform crop at the desired spacing than transplanting. In cool, temperate areas the growing season for bulb onions can be lengthened by raising seedlings for transplanting under protection. Trial crops grown from transplants in Lincolnshire in eastern UK consistently produced bulb yields of 45 t/ha and were 2 weeks earlier maturing than direct-drilled crops, which yielded 30 t/ha on average. In Ontario, Canada it is possible to produce the large, mild, 'Sweet Spanish' type of onion using transplants. In the tropics, small-scale growers can maintain good weed control, a high level of soil fertility using organic manure, well-controlled irrigation and, if necessary, shading to prevent excessive soil temperatures on an intensively managed nursery bed for onion transplants, making this the most practical way of starting the crop (Currah and Proctor, 1990).

In parallel with the developments in direct sowing, new techniques of growing from transplants have also evolved in recent years. Onions are traditionally transplanted as bare-rooted seedlings dug up from nursery beds. More recently, multi-seeded modular transplants have also been used. Here, six to eight onion seeds are sown into a small cell or soil block of a suitable growing medium and, after emergence, each module is transplanted to give a small cluster of plants at each planting station.

BARE ROOT TRANSPLANTING In Ontario, onions for transplanting are sown under glass using 4500 seeds/m^2, either broadcast or in rows about 10 cm apart. Day temperatures of about 17°C and night temperatures of 10°C are maintained. The aim is to produce seedlings with pseudostems 3.5 mm thick about 11 weeks after sowing. Before planting out, the plants are hardened by reducing the frequency of watering and exposing them to temperatures of 4–7°C for a week or so (Riekels *et al.*, 1976). In many tropical regions onions

are started by sowing into small beds of well-manured soil followed by regular watering. Dry grass mulches are often used to protect the soil surface from damage by heavy rain, to conserve moisture and to suppress weeds (Currah and Proctor, 1990).

Premature bulbing of transplants must be prevented. Seedlings that have started to bulb at transplanting can continue to develop small bulbs, cease to grow and enter bulb dormancy prematurely. This occurs where conditions in the seedbed favour bulbing. In temperate regions, late-transplanted crops may experience bulb-inducing photoperiods while still in the seedbed as the days lengthen in spring. In the tropics, seeds sown in summer to provide transplants for early-autumn transplanting are likely to experience high temperatures and photoperiods that induce bulbing. In both situations the high planting density used in seedbeds will increase the tendency to bulb (see Fig. 4.33). In Norway, this problem is prevented in late-transplanted seedlings by decreasing the photoperiod to 12 h during the last half of the transplant-raising period by the use of blackout screens.

To ease handling during transplanting, shoots plus roots are frequently trimmed to a length of 10–15 cm, but experiments have shown that this reduces yields slightly. Transplants are normally planted with the base of the seedling about 2.5 cm below the soil surface. Experiments with the large-bulbed, 'Sweet Spanish' types showed that deeper planting, at 5 or 10 cm, made the bulbs more elongated in shape and reduced the degree of internal doubling. This made the crop more suitable for producing unsplit 'onion rings' when sliced across. The same effect could be achieved by ridging soil around the onions as they grew (Chipman and Thorpe, 1977).

Semi-automatic transplanting machines exist, but yields are lowered if seedlings are not planted upright. Transplanted crops are frequently grown at rather wide spacings, e.g. 20–40 plants/m^2, using a within-row distance of about 10 cm, either because they are to produce large bulbs, e.g. the 'Sweet Spanish' types of North America, or because the layout of ridges and furrows for irrigation or limitations of soil fertility make closer spacing unsuitable.

MULTI-SEEDED MODULE TRANSPLANTING Experiments in Norway (Vik, 1974) showed that satisfactory bulb crops were produced when groups of three to seven seedlings were raised in small pots and transplanted as a cluster in April. During bulbing, the plants pushed each other apart and the resulting bulbs were not misshapen. Plastic trays containing 9–15 ml of loosely filled compost are widely used for raising vegetable seedlings, and are suitable for raising groups of five to six onion seedlings for transplanting. In the UK, the yield of bulbs > 40 mm in diameter reaches a maximum of 45–55 t/ha when modules containing five to six seedlings are transplanted at 10 modules/m^2 (Hiron, 1983). In these conditions, 60–70% of the bulbs are > 60 mm in diameter. Using more seedlings per module, or planting modules at a higher density, reduces mean bulb size. Clearly, using such multi-plant modules reduces the

transplanting effort needed to achieve a particular plant population. In addition to loose-filled trays, 'peat blocks' – cuboid blocks of compressed peat – of various sizes are satisfactory for raising such transplants. Blocks formed to a 27 mm cube by compressing 50 ml of peat-based compost have proved adequate, and little benefit has been found from larger peat blocks.

For loose-filled trays, various compost media may be used, provided attention is paid to nutrient requirements. A mixture of finely milled sphagnum peat mixed with 10% by volume of sand containing ground magnesium carbonate, calcium carbonate, calcium phosphate, potassium nitrate and fritted trace elements has been developed (Hiron and Symmons, 1985). Because of the small volume of compost, extra potassium nitrate liquid feed is needed weekly from the first true leaf stage onwards. Alternatively, small granules of a slow-release fertilizer can be incorporated in the compost. Peat blocks contain more reserves of nutrients, and therefore less frequent liquid feeding is satisfactory.

Seedlings at the 1–2 true leaf stage, satisfactory for planting, are produced in about 200 day-degrees > 6°C from sowing. A sequence of temperatures starting with germination at 18–21°C, progressing down to 10°C then followed by 2 weeks of hardening at ambient temperatures can produce such seedlings 6 weeks after a mid-February sowing in the UK. If soil or weather conditions are not suitable for transplanting, modular transplants can be stored for up to 2 weeks at 0.5°C with 95% RH in the dark, without loss of viability. Before transplanting it is beneficial to give such modules a thorough watering with liquid feed. Irrigation after transplanting is desirable, although not always essential. Dried-out peat blocks can harden and entrap the seedling roots. To avoid this, the tops of the blocks must be covered by soil after planting.

Fertilizer and post-emergence herbicidal requirements are similar to those for a directly seeded bulb crop, but herbicidal treatments immediately after transplanting should be avoided to allow the leaves to 'harden' and develop a normal, waxy coat. The variable costs incurred in establishing a crop in this way in the UK have been calculated as being about 3.5 times greater than for a directly sown crop (Senior, 1982). Higher yields, better quality (e.g. larger mean bulb size), earlier harvesting and more reliable results may make the extra cost worthwhile in areas where the growing season for bulb onions is short.

Sets

Sets are small bulbs, typically weighing 2–3 g when fresh, produced by growing a crop from seed sown at the very high density of 1000–2000 plants/m^2. They are < 25 mm diameter and are planted to develop into larger bulbs. Because of their size, sets make a more robust plant at emergence than seeds, and do not need such meticulous seedbed preparation. They are therefore easier to grow successfully and are widely used by amateur and small-scale growers. Sets also have a shorter growing season than plants from seeds and are used where rapid, early-season production is important.

In The Netherlands, the main set-producing country for Europe, seed is sown in early April at a rate of about 10–12 g/m^2 in rows 15–20 cm apart using seed drills with coulters (part of the seed drill) that spread the seed into a band 7–10 cm wide.

Sets have the potential to transmit diseases and pests, and for this reason The Netherlands government runs an inspection regime to ensure that land used for set production is free of the stem and bulb eelworm, *Ditylenchus dipsaci* and onion white rot, *Sclerotium cepivorum* (see Chapter 5). The crop is grown with a low level of N fertilizer – normally just 40 kg/ha or less – to encourage 'hard growth'. At harvest, which is earlier than a normal bulb crop because the high density promotes early bulb initiation and foliage fall-down, the leaves are mown off, the crop is undercut, windrowed (air-dried) and then picked up and transferred to a store for rapid drying in a draught at 20–25°C. Thereafter, they are ventilated with unheated air until fully dry. Sets can be stored in bulk to a depth of up to 3 m. The sets of the widely grown, bolting-resistant cvs 'Stutgarter' and 'Sturon' are stored through the winter at 3–4°C.

To ensure that sets from other, normally seed-grown cultivars do not bolt following planting out, high temperature storage at about 28°C is desirable from November to March. Large sets, > 20 mm in diameter, may need warm storage until April to prevent bolting. In general the smaller the set, the less is the likelihood of bolting. High-temperature storage also increases vigour, delays maturity and increases yield. Relative humidity of 60–70% is necessary to prevent excessive moisture loss during high-temperature storage but, in spite of this, 10–25% weight loss occurs.

A novel technique has been developed for producing 'mini-sets' only 8 mm in diameter, which utilizes surplus glasshouse capacity following the UK transplant-raising season. Seeds are sown in early June into cellular trays, as for transplant production, with five to six seedlings per module and left in the glasshouse to produce ripe mini-sets by August. After winter storage at 27°C, a high yield was produced from spring planting. Furthermore, these sets are so small that they can be sown with an ordinary seed drill adjusted for a large-seeded crop like beans.

In warm regions like Israel and Pakistan, sets produced from a spring sowing are replanted in the late summer to produce a quickly maturing bulb crop for harvesting in December. In Israel, seeds of cv. 'Bet alpha' are sown in February and harvested as sets in April. The sets are planted in July or early August and bulbs are harvested in December. During this growing season photoperiods decline from 14 to about 10 h. Cultivars with a slightly longer day-length requirement for bulbing than 'Bet alpha' revert to leaf growth and fail to complete bulbing when grown in this way (Corgan and Kedar, 1990). The more rapid bulbing of sets compared with seedlings of the same cultivar (Fig. 4.33) may also be important here.

At high latitudes with a late spring and a short growing season, the rapid production of a bulb crop is possible by using sets. In Norway, large sets are used to produce early bulb crops (Vik, 1974).

In general though, sets should be 1–2 cm in diameter; those < 16 mm in diameter rarely flower. Larger sets can bolt, particularly if exposed to long periods at cool temperatures (7–12°C) before they start to bulb. Large sets also have a greater tendency to produce split, double bulbs.

Set-planting densities of 30–80/m^2 are typical, with the exact density depending on the bulb size desired. Ideally, sets should be planted upright and only just covered with soil. When planted by machine, the sets are dropped into shallow furrows and are not uniformly upright. Yield reductions of 10–30% have been attributed to non-upright planting when machine-planting has been compared with hand-planting. Firming of soil over the planting furrows with a press wheel following the planting of sets can improve the emergence and yield. Possibly, improved capillary movement of water to the base of the sets in firmed soil promotes sprouting.

Post-establishment culture

Once an onion crop has been planted, has emerged and is satisfactorily established, the grower should try to promote a rapid but even rate of growth. With spring-sown crops at high latitudes the length of the growing season is limited, and any delays in growth may reduce yields or delay bulbing until photoperiods and temperatures cease to be conducive to its completion, resulting in non-ripening, thick-necked plants (see Fig. 6.11). In autumn-sown crops, checks to growth act like delays in sowing date and result in smaller bulbs and lower yields. This is because Leaf Area Indices (LAIs) will be lower at the time when inductive photoperiods cause leaf growth to cease because of bulbing. Uneven growth rates late in development can lead to split skins on bulbs that resume growth after the hard, dry outer skins have already started to form. Factors partially within the grower's control include weed competition (see Chapter 5), water supply and nitrogen nutrition.

Irrigation requirements

Several features of the root systems of edible alliums are important in conditioning their response to both soil water and nutrients (de Melo, 2003): they have a shallow rooting depth, with nearly all roots within 40 cm of the surface, and individual roots are comparatively thick and sparsely branched (see Figs 2.15 and 2.16). As seedlings develop, adventitious roots arising from the stem base supersede the primary root and give rise to most of the root system. The shallow, sparse root system means that a relatively small volume of soil water is available before evapotranspiration rates become limited by soil water supply. Among the commonly grown crops only a few other vegetables – namely, celery, spinach, lettuce and radish – are as limited as onions and garlic in this respect (see Allen *et al.*, 1998, Table 22). To keep these crops growing at

their maximum potential rate with evapotranspiration – and hence photosynthesis and growth – unchecked by soil water supply requires more frequent irrigation than for deeper and more densely rooted crops.

The need for frequent irrigation and a shallow rooting depth means that nutrients – in particular, nitrate, which exists solely in the soil solution – are easily leached below the rooting depth if water enters soil already at field capacity as a result of rainfall or uneven irrigation. Great importance is now placed on minimizing such losses of nitrate so as to avoid pollution of aquifers and rivers. For these reasons, edible alliums are demanding crops in terms of the irrigation and nutrient management needed to achieve maximum yields with minimum losses of water and nutrients to leaching or run-off. The following sections will outline the fundamentals underlying optimum management and some of the methods available for achieving near-optimal results in varying circumstances.

FUNDAMENTALS OF IRRIGATION The principles underlying the irrigation requirements of crops, including onions and garlic, are described by Allen *et al.* (1998). Transpiration is essentially the physical process of water evaporation from moist surfaces within the leaves into the atmosphere via the stomata on the leaf epidermis. In a field situation, evaporation directly from moist soil to the atmosphere also occurs and is particularly important when leaves do not cover much of the ground – for example, when a crop is small soon after emergence.

Evaporation of water requires large amounts of energy, which is derived from solar energy influx, either directly as radiant energy or indirectly as sensible heat. Therefore, evapotranspiration is governed by energy exchange and is limited by the amount of energy available. From the principle of energy conservation it is possible to predict evapotranspiration rates, since the energy arriving at the surface must equal the energy leaving it during the same period. Another method of estimating evaporation is the mass transfer method that considers the transport of water vapour and energy (heat and momentum) to and from evaporating surfaces in small parcels of air, termed eddies.

Making certain assumptions, evapotranspiration can be calculated from vertical gradients of air temperature and water vapour concentration above crop surfaces. The energy balance and mass transfer methods have been combined to derive the Penman-Monteith equation, which can be used to calculate the evaporation from a uniform expanse of vegetation using parameters that can be measured or calculated from weather data. The resistance to evaporation in this equation depends on stomatal behaviour and the 'architecture' of the crop surface, in terms of its height and surface roughness. To simplify this situation, the resistances of different crops have been computed relative to evapotranspiration from a standard large, uniform expanse of grass with a height of 0.12 m, a fixed surface resistance of 70 s/m and an albedo (see below) of 0.23.

Evapotranspiration from this standard reference surface is denoted as ET_0 (mm/day of water). ET_0 is a function of the net daily radiation at the crop surface, the daily soil heat flux density, the mean daily air temperature and wind speed at 2 m height and the mean daily water vapour pressure in the air. Thus ET_0 incorporates the effects of weather conditions on evapotranspiration. Allen *et al.* (1998) recommend the Penman-Monteith equation, since it allows ET_0 to be unambiguously determined to provide consistent values in all regions and climates using readily measured meteorological data.

Characteristics that distinguish a particular crop species from the reference crop are integrated into the 'crop coefficient', K_C. The evaporation from a disease-free, well-fertilized crop grown in large fields without water stress, ET_C, is predicted by multiplying ET_0 by K_C:

$$ET_C = ET_0 K_C \qquad \text{(Eqn 6.8)}$$

The crop coefficient can be divided into two components: K_{CB}, 'the basal crop coefficient' for evaporation from the crop leaves and K_E for evaporation from bare soil between plants; therefore:

$$K_C = K_{CB} + K_E \qquad \text{(Eqn 6.9)}$$

The crop coefficient integrates the effects of four main characteristics that distinguish a crop from the reference grass: (i) crop height, which influences resistance to water vapour transfer from crop to atmosphere; (ii) the reflectance (albedo) of the crop–soil surface, which influences the net radiation absorbed; (iii) the canopy resistance of the crop to vapour transfer, which varies with leaf area and the degree of stomatal control; and (iv) the evaporation from soil. The K_C of well-grown onion and garlic crops at their maximum leaf cover is fairly close to unity (see Table 6.3), and hence allium crop evapotranspiration, in common with that of other short vegetables, is similar to the grass reference evapotranspiration, ET_0.

Similar values probably apply to leeks and Japanese bunching onions, given their similarity of root and shoot morphology to the crops in Table 6.3. The K_C and K_{CB} values in Table 6.3 are those expected under a standard climatic condition defined as sub-humid with a mean RH of 70%, a minimum RH of 45% and moderate wind speeds averaging 2 m/s. K_C depends to a degree on climate, increasing as wind speed increases and humidity decreases and decreasing at low wind speeds and high humidity, to give a range for onions of 0.94–1.22 around the value of 1.05 for the standard climate (see Fig. 6.12).

When a crop is small and hardly shading the ground, K_C depends largely on soil evaporation, and this decreases drastically as the soil surface goes from wet to dry. The K_C for wet soil may exceed 1.0, but a dry soil surface can have a K_C as low as 0.1. As a crop develops, K_C will change as the proportion of leaf cover to bare soil increases. For evapotranspiration calculation purposes, values of K_C are divided into four phases: (i) 'initial', from sowing to 10% ground cover; (ii) 'crop development', from 10% ground cover to full leaf cover; (iii) 'mid-season',

Table 6.3. Crop parameters affecting the evapotranspiration of edible alliums (from Allen *et al.*, 1998).

Crop species	Height (m)	K^a_{Cmid}	K_{Cend}	K_{CBinit}	K_{CBmid}	K_{CBend}	Maximum rooting depth[b] (z_r, m)	Depletion fraction for RAW[c] (p)[d]
Garlic	0.3	1.00	0.70	0.15	0.90	0.60	0.3–0.5	0.3
Bulb onion	0.4	1.05	0.75	0.15	0.95	0.65	0.3–0.6	0.3
Green onion	0.3	1.00	1.00	0.15	0.90	0.90	0.3–0.6	0.3
Seed onion	1.05	1.05	0.80	0.15	1.05	0.70	0.3–0.6	0.35

[a]All the K values apply to a temperate sub-humid climate with a minimum RH of 45%, a mean RH of 70% and moderate windspeeds averaging 2 m/s at 2 m height.
[b]The larger values of z_r are for soils with no restriction to rooting and apply to water-stressed or rainfed crops; the smaller values are appropriate for irrigation scheduling.
[c]RAW is the 'readily available water' fraction of water in the soil at field capacity. When water is depleted below RAW, K_{CB} is reduced by a stress factor K_S (see Eqns 6.11 to 6.14).
[d]The p values apply to a medium-textured soil at ET_0, approximately 5 mm/day.
Formulae to adjust K and p values for different climatic conditions are given in the text.

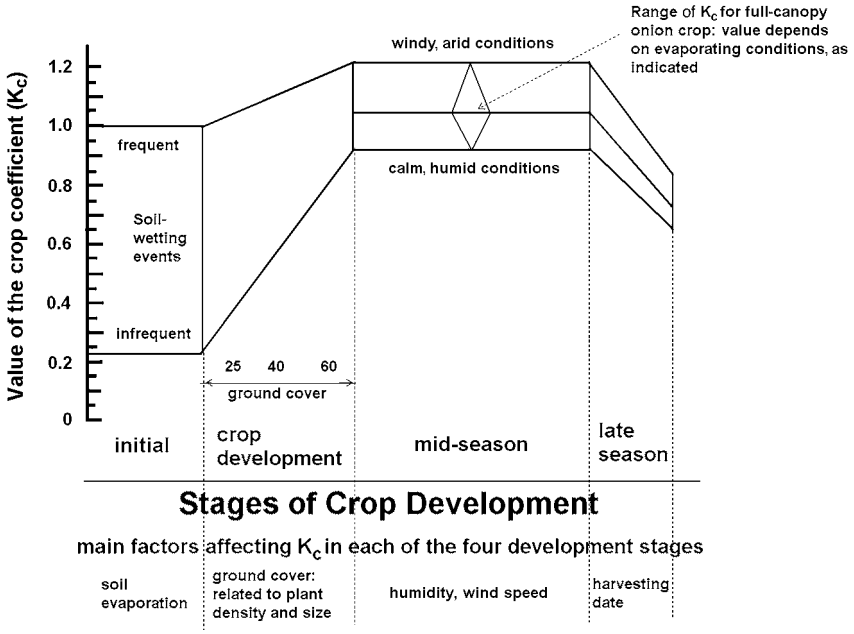

Fig. 6.12. Values of the crop coefficient for evapotranspiration, K_c (see Eqns 6.8 and 6.9) for well-fertilized bulb onion crops growing in a large field without water stress. Values of K_c change with the stage of crop development and vary with the frequency of soil surface wetness, particularly during early growth and with climatic condition (see Eqn 6.10 and Table 6.3) (diagram based on Allen *et al.*, 1998, Fig. 24, and data for onions given by these authors in their Chapters 5 and 6).

from full cover to the start of maturity; and (iv) 'late-season', from the start of maturity to senescence or harvest.

Figure 6.12 shows how K_C for a bulb onion crop changes through these growth stages and how K_C values range depending on the frequency of soil wetting, the humidity and wind speed. For directly sown onions and leeks the initial stage is comparatively long because of their slow germination, small emergence weight and low RGR compared with many crops. It is usually necessary to keep the soil moist before emergence, so values of K_C typical of wet soil (i.e. close to 1.0) will occur. The duration of the initial and crop development phases can be predicted using models based on day-degrees or effective day-degrees (Eqns 4.7 and 4.18). The duration of the mid-season and late-season phases will also depend on climate, tending to be shorter the warmer the conditions (see Fig. 4.4a).

In Eqn 6.9 K_{CB} represents the ratio of crop evaporation to the reference grass evaporation when the soil surface layer is dry but where there is adequate water in the root zone for maximum transpiration rate. During the mid- and

late-season stage K_{CB} is about 0.1 lower than K_C for the allium crops (see Table 6.3), which is typical of vegetable crops where the ground cover by leaves may be 80% or less (Allen *et al.*, 1998, Table 18). K_{CB} values can be adjusted for climate using the formula:

$$K_{CB} = K_{CBT} + [0.04(u_2 - 2) + 0.004(RH_{min} - 45)](h/3)^{0.3} \quad \text{(Eqn 6.10)}$$

where

K_{CBT} = value of K_{CB} for the temperate, sub-humid climate given in Table 6.3

u_2 = mean value of daily wind speed 2 m above grass (m/s) for $1 < u_2 < 6$m/s

RH_{min} = mean value of daily minimum RH, provided $20\% < RH_{min} < 80\%$

h = mean plant height, m.

Prior to the mid-season stage, K_E makes a substantial contribution to K_C (see Fig. 6.12), depending on both the frequency of soil wetting and the quantity of water wetting the soil, the evaporating power of the atmosphere (ET_0) and the texture of the soil. Finer-textured soils hold more water and carry on releasing water for evaporation for longer following a wetting to field capacity. As well as soil and weather factors, K_C depends on the fraction of the soil surface that is wetted by irrigation, and whether or not the wetted fraction is covered by the leaves. Under drip irrigation (see below) the wet fraction of the soil surface is frequently shaded by leaves, and K_C can remain low even after irrigating, whereas with furrow irrigation it is likely that the wet fraction of the soil will be partly unshaded, and this will give rise to an increase in K_C following irrigation. Allen *et al.* (1998) describe how to compute daily values of K_C for a particular crop with its unique pattern of rainfall plus irrigation, soil texture and ET_0 in order to schedule the irrigation of the crop.

THE EFFECTS OF WATER STRESS ON EVAPOTRANSPIRATION As soil dries, the soil water becomes less free to move and is more strongly bound. When the soil reaches a certain dryness, water can no longer move to roots at sufficient rate to satisfy the potential evapotranspiration (ET_C), and the crop is said to be water stressed. In these conditions stomata close and restrict gas exchange, and the transpiration rate falls below its potential rate. The effects of water stress on evapotranspiration can be described by adjusting the basal crop coefficient by a water stress coefficient, K_S (Eqn 6.11).

$$ET_{Cadj} = (K_S K_{CB} + K_E)ET_0 \quad \text{(Eqn 6.11)}$$

The total available water (TAW) to a crop depends on the rooting depth and the volume of water held between field capacity and the wilting point per unit volume of soil. This can vary from about 0.05 for a coarse sand to 0.20 (m^3/m^3) for a silt or clay. The fraction of available water that a crop can extract without any restriction in transpiration rate (i.e. without stress) is termed the readily available water (RAW) (Eqn 6.12).

$$RAW = p\ TAW \quad \text{(Eqn 6.12)}$$

Thus p is the average fraction of total available water that can be depleted before moisture stress occurs. Rooting depths and p values for alliums are given in Table 6.3. These rooting depths and p values are low compared with those of other crop species, a consequence of their shallow rooting habit and low root length per unit volume of soil (see Chapter 2). p depends on the potential crop evapotranspiration rate, ET_C. p decreases as ET_C increases, and increases with a decreasing ET_C (Eqn 6.13).

$$p = p_{Table6.3} + 0.04(5 - ET_C) \quad \text{(Eqn 6.13)}$$

The soil texture also has an effect, with p values being 5–10% lower for clay soils and 5–10% higher for sandy soils. Volumes of total available water, TAW and readily available water, RAW, for fully grown bulb onion crops on a typical range of soils are contrasted with values for maize in Table 6.4. To avoid yield restrictions, water depletion should not fall below RAW, and it can be seen how this requires more frequent irrigation for onions than maize and on sand rather than on silt soils.

Below RAW – i.e. when the soil water deficit is greater than p (root zone water depletion, $D_r > RAW$) – transpiration can be assumed to decrease linearly towards zero at permanent wilting as K_S, the stress adjustment factor, decreases from unity towards zero (see Fig. 6.13); therefore:

$$K_S = (TAW–D_r)/(TAW–RAW) = (TAW–D_{r)}/[(1–p)TAW] \quad \text{(Eqn 6.14)}$$

D_r = root zone water depletion mm, estimated from the daily soil water balance

TAW = total available water mm

K_S from Eqn 6.14 above can be used in Eqn 6.11 to compute the evapotranspiration adjusted for water stress, ET_{Cadj}.

For maximum growth rate, irrigation should be applied before D_r falls below RAW, but the amount of water applied should not exceed D_r, in order to avoid leaching nutrients from the root zone.

EVAPOTRANSPIRATION AND YIELD Bulb yields increase linearly with evapotranspiration (see Fig. 6.14a). The yield response factor, K_Y, the relative

Table 6.4. Values of Total Available Water (TAW) and Readily Available Water (RAW) (mm) for a bulb onion and a maize crop on contrasting soil textural types (from Allen *et al.,* 1998).

	Rooting depth Z_r (m)	Depletion fraction for RAW p[a]	Loamy Sand		Silt		Silty clay	
			TAW	RAW	TAW	RAW	TAW	RAW
Onion	0.4	0.30	36	11	68	20	48	14
Maize	1.2	0.55	108	59	204	112	144	79

[a]The p value applies to the standard climatic conditions given in Table 6.3.

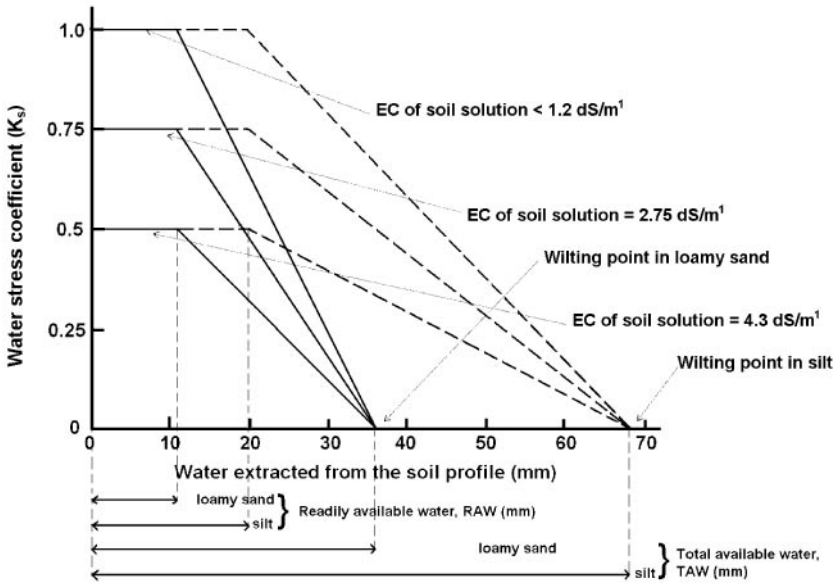

Fig. 6.13. The effects of water stress caused by the depletion of soil water and/or soil solution salinity on the water stress coefficient, K_S, which quantifies the stress-caused decrease in crop evapotranspiration (see Eqns 6.11, 6.14, 6.15 and 6.16). (NB: this graph and the equations (6.15 and 6.16) on which it is based are only approximate and are unlikely to hold when salinity and water depletion from the soil exceed levels needed to reduce yields by 50%) (based on Allen *et al.*, 1998, Fig. 44, with data from their Table 23 and the effects of soil type on available water given in their Example 36.)

decrease in yield per unit relative deficit in E_{TC}, during the bulbing phase is 1.5 (see Fig. 6.14b; Duranbos and Kassan, 1979; Al-Jamal *et al.*, 2000). Over the whole growing season, K_Y for onions is 1.1 (Duranbos and Kassan, 1979). The larger yield response factor for the bulbing period reflects the fact that yields are particularly sensitive to water stress at this stage (Bosch-Serra and Currah, 2002).

WATER STRESS CAUSED BY SALINITY The tolerances of crops to salts in the soil have been characterized in terms of the electrical conductivity of the solution from soil saturation extracts, EC_e, which first reduces yield below its full potential ($EC_{ethreshold}$) and as the slope (b) of the reduction in crop yield with increase in salinity beyond this threshold (Allen *et al.*, 1998). Onions have an $EC_{ethreshold}$ of 1.2 dS/m (deciSiemens/m) at 25°C and a 16% reduction in yield per 1 dS/m increase in conductivity beyond the threshold, making them, next to beans, the most sensitive common field crop in this respect (Allen *et al.*, 1998, Table 23).

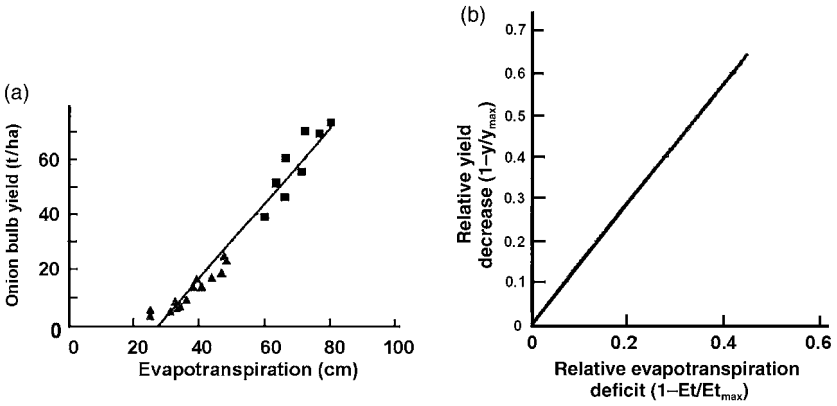

Fig. 6.14. Relationships between onion bulb yields and crop evapotranspiration during the bulb growth phase on a sandy loam soil at Farmington, New Mexico, USA. (a) Total bulb yield as a function of crop evapotranspiration: (▲), 1986 data; (■), 1987 data; the line is fitted to both years' results. (b) The relationship between relative yield decrease and relative evapotranspiration deficit; the yield response factor to crop evapotranspiration, K_Y, is the slope of this line (from Al-Jamal *et al.*, 2000. Courtesy of *Agricultural Water Management*).

Since yield reductions caused by water stress are proportional to the reduction in transpiration caused by water stress (see above), Allen *et al.* (1998) used this relation combined with Eqn 6.14 to derive a stress factor K_S to describe how salinity – and also combined salinity and soil water stress – will reduce transpiration.

When $EC_e > EC_{ethreshold}$ and $D_r < RAW$:

$$K_S = [1 - (b/100K_Y)(EC_e - EC_{ethreshold})] \quad \text{(Eqn 6.15)}$$

When $EC_e > EC_{ethreshold}$ and $D_r > RAW$:

$$K_S = [1 - (b/100K_Y)(EC_e - EC_{ethreshold})][(TAW - D_r)/(TAW - RAW)] \quad \text{(Eqn 6.16)}$$

K_Y is the yield response factor (see Fig. 6.14b).

These equations are only approximate estimates of the long-term impact of salinity on ET_C and are unlikely to hold where EC_e and D_r values exceed those needed to reduce yields by 50% (Allen *et al.*, 1998). Figure 6.13 illustrates how these equations predict that water stress and salinity together affect K_S, and therefore the transpiration rate, of onion on contrasting soil types.

Factors other than water stress and salinity can reduce the LAI to below that of a well-grown crop (i.e. < 3 in mid-season), resulting in lower transpiration. For example, pest, disease or hail damage or low plant density resulting from such damage or from poor seedling establishment may all reduce LAI. Allen *et al.* (1998) give equations to estimate the consequences for evapotranspiration of

such non-pristine foliage. Although the total transpiration will be less than for a well-grown crop, low LAIs have increased transpiration rates per unit leaf area due to more micro-scale transfer of heat from dry soil surfaces to the leaves and to a higher aerodynamic roughness.

IRRIGATION TECHNIQUES AND EXPERIMENTS Onion crops are grown using furrow, sprinkler and trickle irrigation. Furrow irrigation involves inundating furrows adjacent to raised beds on which onions are planted, using systems of channels and small sluices. If salinity is a problem, onions may be planted on the side of raised beds, since salts reach a maximum concentration at the apex of the bed after being drawn there by evaporation.

Various types of sprinklers are used on onions, including centre pivots, moving gantries or fixed lines. If onions are directly sown, frequent light sprinkler irrigation is often necessary to ensure rapid and even emergence by keeping the seeds and seedlings hydrated and preventing the formation of a dry, impenetrable crust on the soil surface. In areas prone to salinity it is important to avoid a salty 'crust' developing after frequent light irrigation, as this is particularly damaging to emerging seedlings (Miyamoto, 1989).

Beginning in the early 1990s, onion and garlic crops have been produced using plastic 'drip-lines' to supply water and, often, dissolved fertilizer (N, and sometimes N and K); the latter is termed 'fertigation'. Particularly in semi-arid regions, these techniques have led to dramatic increases in yield. For example, in the Treasure Valley of eastern Oregon, USA, yields above 115 t/ha of long-storing, 'Sweet Spanish' onion bulbs can reliably be produced under drip fertigation, up from 70 t/ha under furrow irrigation (Shock *et al.*, 2004).

Near Lleidda, in north-eastern Spain, yields of 90 t/ha of bulbs (equivalent to 11–13 t/ha of dry matter) are produced, up from 50 t/ha under sprinkler irrigation (Bosch-Serra and Currah, 2002). Garlic yields of 30–40 t/ha are achieved under drip fertigation in Mexico, three times previous yields, and the larger bulb sizes achieved have necessitated a re-evaluation of optimum densities and clove sizes for planting (Castellanos *et al.*, 2004). Onion growers using fertigation have received a price premium for the very large bulbs produced. In Oregon the increasing sizes are reflected by a progression of superlatives to name the grades marketed: i.e. bulb diameters 76–102 mm, Jumbo, 102–108 mm, Colossal, > 108 mm, Super Colossal.

Drip-lines may be laid on the surface or buried 10–15 cm deep in the soil. In the system described by Shock *et al.* (2004), drip tapes were installed at a depth of 13 cm between double rows of onions spaced 0.56 m apart on beds 1.1 m wide. The drip tape had emitters spaced 30 cm apart, with a flow rate of 0.5 l/h. Fertilizers other than N were incorporated into the silt–loam soil before bed formation in amounts determined from soil analysis. N fertilizer was applied through the drip-tape as urea-ammonium nitrate on five occasions at 10 day intervals during the main period of leaf growth. Soil water potential was measured by sensors 20 cm below the onion rows. The mean soil water

potential of the sensors was monitored every 3 h and, if this fell below –20 kPa, 1.5 mm of irrigation was applied. Using this system the soil water potential at 20 cm depth was held close to –20 kPa, and the cumulative water applied plus rainfall closely matched the evapotranspiration of the crop calculated using a modified Penman-Monteith formula (see Fig. 6.15).

An earlier trial (Shock *et al.*, 2000) established that a water deficit of –20 kPa at a depth of 20 cm was about optimal. A lower water stress resulted in more bulbs rotting in store in some seasons and less efficient use of water, with more leaching. Yields – particularly of colossal grades – decreased at greater water stress (see Fig. 6.16a).

In north-eastern Spain, at plant densities greater than 40 plants/m^2, bolting was a serious problem that was associated with the high early LAIs of high-density, fertigated crops (Bosch-Serra and Currah, 2002). Increased yields from drip-line at fertigated onion crops have been reported from Poland (Rumpel *et al.* 2003), but no improvement of drip-fertigation over conventional sprinkler

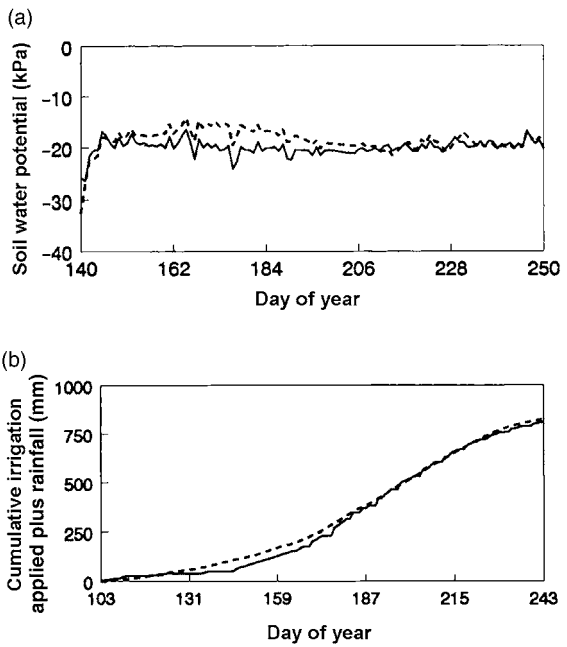

Fig. 6.15. Soil water potentials and cumulative total water received compared with calculated crop evapotranspiration for sub-surface, drip-fertigated bulb onions growing in the Treasure Valley of eastern Oregon, USA. (a) Measured soil water potentials at depths of 20 cm (solid line) and 46 cm (broken line) for onions drip-irrigated automatically when a sensor at 20 cm depth measured a soil water potential of –20 kPa. (b) The cumulative water applied plus rainfall (solid line) and the calculated crop evapotranspiration, ET_C, (broken line) of this irrigation regime (from Shock *et al.*, 2004. Courtesy of *HortScience*).

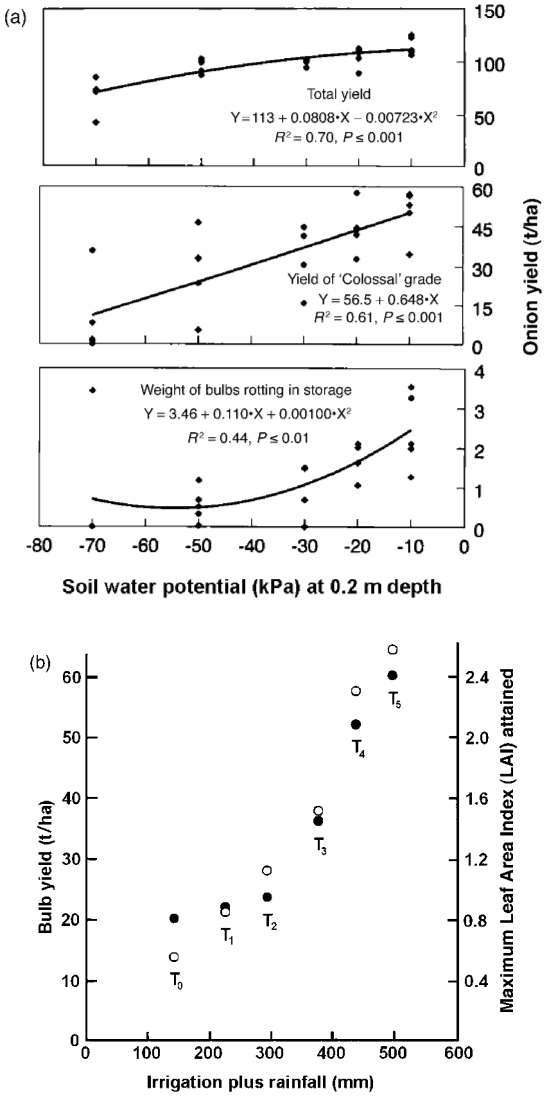

Fig. 6.16. Responses of bulb onion yields to irrigation. (a) The effect the soil water potential maintained at a depth of 0.2 m on the total bulb yield, the yield of 'Colossal' grade (> 102 mm diameter) bulbs and the yield of bulbs rotting in storage by 15 December for onions grown using drip fertigation in the Treasure Valley of eastern Oregon, USA (from Shock *et al.*, 2000. Courtesy of *HortScience*). (b) The response of bulb yield and Leaf Area Index (LAI) to irrigation for onions grown at a density of 25 plants/m^2 at Albacete, Castilla-La Mancha, Spain. The treatments T_0, T_1, T_2, T_3, T_4 and T_5, respectively received irrigation equal to 20, 40, 60, 80, 100 and 120% of the crop evapotranspiration, ET_C, calculated on the basis of Eqn 6.8 (see text) (from Martin de Santa Olalla *et al.*, 1994).

irrigation was reported for sweet 'Vidalia' onions in Georgia, USA, in terms of either yield or reduced bulb rot (Diaz-Perez *et al.*, 2004; Gitaitis *et al.*, 2004).

On a sandy-loam soil in Colorado, USA, yields from drip-lines at 8 cm depth in the centre of 40 cm-wide four-row beds were lower than for sprinkler-irrigated onions, unless large amounts of water in excess of ET_C were used to wet the soil profile to the full width of the beds. In the absence of this excess water, soil at the root plate of the outer rows of onions was too dry for adventitious root development (Al-Jamal *et al.*, 2001). It seems that the soil texture, with its associated water conductivity, is a factor in determining the success of drip-lines and their appropriate depth and spacing.

The results of experimental studies of onion crop responses to irrigation are variable. On the one hand it is clear that in many arid zones where the crop is grown, e.g. New Mexico, USA, virtually all the water needed is supplied by irrigation (Corgan and Kedar, 1990). In other regions rainfall is sometimes adequate and yields may actually be decreased by irrigation – for example, if nitrogen is leached from the root zone (Brewster, 1990b).

Crop evapotranspiration, ET_c, calculated using modified Penman-Monteith equations (see Fundamentals of irrigation, above) has proved a reliable basis for scheduling irrigations. Studies have generally shown increases in yield with increases in irrigation applied of up to 100% of ET_c (Kruse *et al.*, 1987; Shock *et al.*, 2000; Al-Jamal *et al.*, 2001) or even 120% of ET_c (see Fig. 6.16b; Martin de Santa Olalla *et al.*, 1994). Excessive irrigation will result in leaching and nitrate loss, and may promote rotting disease in storage (see Fig. 6.16a).

Water productivities in various irrigation studies are shown in Table 6.5. The experiments in Table 6.5 were carried out in fairly arid climates, mostly at a fairly low plant density, so the soil surface evaporation component of ET_c (see Fundamentals of irrigation, above) would be quite large, since much of the soil would not be covered by leaves even at full crop development. In general, it appears that drip irrigation is more efficient in water use than sprinkler or furrow irrigation and that furrow irrigation measurements on farm fields were well below experimental plot values. Furrow irrigation is likely to have the greatest proportion of wet soil unshaded by leaves and the buried drip-lines are likely to have the least, and this is probably the major cause of the differences in water productivity. The high water productivity achieved by Bosch-Serra probably results from the high crop density, resulting in a high proportion of transpiration to evaporation in the overall ET_c.

Irrigation and adequate N during leaf and early bulb growth ensures that an onion crop reaches a high LAI as quickly as possible. This will tend to promote rapid bulb ripening and good bulb quality for storage (see Fig. 4.33). Irrigation and N applications late in bulbing may delay maturity and reduce bulb quality by virtue of skin splitting and rotting, particularly if they follow a period in which growth has been restricted by a lack of water or N. A cessation of irrigation some 2 weeks before harvest has frequently been recommended as promoting bulb ripening and ease of harvest (Brewster, 1990b).

Table 6.5. Water productivities of onion crops under different methods of irrigation.

Author(s)	Type of irrigation	Plant density (plants/m^2)	Water productivity for bulbs (FW/ET$_c$, kg/m^3)	Water use efficiency for bulbs (DW/ET$_c$, Kg/m^3)	Notes
Al-Jamal *et al.* (2001)	Furrow	NA	4.60	0.49	On commercial fields
Al-Jamal *et al.* (2001)	Sprinkler	28.4	8.40	0.90	
Ells *et al.* (1993)	Furrow	NA	9.70	NA	
Martin de Santa Olalla *et al.* (1994)	NA	25	12.20	1.10	
Shock *et al.* (2004)	Drip	25	12.40	NA	Fertigation
Shock *et al.* (2004)	Drip	35	15.00	NA	Fertigation
Bosch-Serra (1999)	Drip	80	19.15	1.61	Fertigation

NA, not available.

Harvesting

The harvesting techniques suitable for bulb onions depend upon weather at harvest time. In areas where warm, dry weather occurs reliably, the curing and bagging of the crop can be done in the field. In wetter, temperate regions, mechanical harvesting and artificial heating and ventilation for drying are essential to produce reliably high quality bulbs on a large scale. The purpose of curing is to dry the neck of the bulb so that it seals, and prevents the entry of disease organisms, and to produce dry, well-coloured outer skins that are not split.

The traditional method of harvesting involves pulling the bulbs from the soil, or undercutting them, and then laying them in rows (windrows) on the ground to dry and cure. In areas with strong sunshine the bulbs must be protected from direct insolation by covering them with leaves while lying outside, otherwise they can be damaged by 'sunscald', which kills the outer soft scale tissue, disfigures the bulbs and may allow bulb-rotting organisms to develop. The bulbs may be left in such rows for 1–2 weeks before removing the foliage and packing in crates or sacks.

If the onions are fairly mature, with soft, near-dry necks, then in dry climates the foliage may be removed when the bulbs are pulled from the soil and the bulb necks left to dry in rows or in stacks of trays (Jones and Mann,

1963). If the bulb skin is wetted after harvest, particularly if it is covered by decaying leaves, fungal growth (*Botrytis cinerea*) may result in dark staining of the skins. Also, moisture on the base of the bulb promotes rooting, which in turn accelerates bulb sprouting (see Chapter 7). Therefore, the appearance and storage potential of field-dried crops in temperate regions is unpredictable.

In the UK and The Netherlands, most bulbs are now dried artificially. The crop is ready for harvest when 50–80% of the plants have soft necks and the foliage is starting to collapse (see Fig. 6.10). The leaves are then mown off and removed using a forage harvester. Then, if the weather is fine and dry the bulbs are left for several hours for the necks to partially dry. The bulbs are undercut with a blade being run under the plants and they are elevated into a trailer. Either at this point or as they are loaded into bulk stores, any weeds, stones and clods are removed. In stores the bulbs are piled on slatted floors to a depth of 3.5–4.0 m. In the UK, ventilating air at a temperature of 25–30°C and 25–35% RH is then blown through the stack at a flow rate of 425 m^3/h/t to remove surface moisture rapidly and dry the necks, thereby preventing skin staining and neck rot infection (see Chapter 5).

When the onions are surface dry so that the skins rustle, the ventilating air is recycled and dry outside air is introduced sufficient to maintain RH below 75%. A continuing slow drying at 25–30°C and 70–75% RH ensures that the necks are fully dry and that the bulb skins develop a deep, copper-brown colour; this normally takes 10–15 days. Exposure to temperatures above 21°C causes the skins to darken: the higher the temperature above 21°C the more quickly the skins darken (see Chapter 7, 'Curing of Bulb Skins').

In The Netherlands bulbs are ventilated with air at 20–25°C during the neck-drying phase because lighter-coloured, yellow-brown skins are preferred. It has been shown that high-temperature curing, particularly if applied to bulbs that are not fully ripe, may shorten storage life (see Chapter 7). When the necks are fully dry, the temperature of the stack of bulbs is lowered as quickly as possible using cool air drawn from outside at night, and the bulbs are subsequently maintained as cool as possible, but above freezing, while in store. Because of the need for even ventilation through the stack, it is important that the air flow is not obstructed by pockets of soil or weed trash. Such obstructions can give rise to clumps of undried, uncured bulbs that soon begin to rot and spread damaging, wet, rotten conditions to surrounding bulbs.

The extent of damage tolerable and therefore the harvesting and storage facilities that are appropriate and economic depends on the type of bulb being processed. Considerable effort has gone into researching improved mechanical harvesting and storage of soft, thin-skinned, high-priced, sweet onions from Georgia, USA (Maw *et al.*, 1998, 2002). Mechanical harvesters that pick up the onions by their leaves after undercutting rather than with an elevator, as used for hard 'storage'-type bulbs, have been developed for this valuable crop, which is easily damaged and subject thereby to losses and rots, and for which it is a necessity to maintain consistently high quality to justify premium prices.

The optimum harvest date has been investigated in several studies (see Brewster, 1990b). All experiments show that bulb yield continues to increase until well after foliage fall-down, probably while the leaves remain at all green; this is normally for at least 2 weeks after fall-down. However, most studies show that the time to sprouting is maximum when plants are harvested at 50–80% fall-down. Earlier or later harvest results in earlier sprouting in store. Also skin quality, as shown by staining and splitting, deteriorates if bulbs are harvested at a later stage, particularly if the weather is wet. Therefore, the date of harvest is a compromise between maximum yield and maximum storage life and skin quality. Skin quality has assumed great importance in Europe recently, and therefore bulbs are normally harvested at the 50–80% foliar fall-down stage. In the warm, dry climate of California, experiments have shown maximum storage life and least rotting in store when bulbs were harvested when the foliage was fully senesced, well after fall-down (Currah and Proctor, 1990). Therefore, in dry climates the optimum stage for harvest may be later than in wetter, cooler regions.

SEED PRODUCTION

Onion seed production

The physiology of flowering finds its most important application in seed production. This has been reviewed by Peters (1990), pollination biology in seed production by Currah (1990) and seed production in tropical regions by Currah and Proctor (1990). Seed yields of about 500 kg/ha are common in many regions, but in the USA 800–1000 kg/ha are typical. In trials in California, seed yields from bulbs stored at optimum pre-planting temperatures varied almost fourfold from year to year, with a maximum yield of 1554 kg/ha (Jones and Emsweller, 1939). Yields of more than 3000 kg/ha have been obtained in experiments using high plant densities and irrigation in Washington State, USA (Vincent, 1960). In contrast, the best trial yields of seeds from a multiplier cv. in the Philippines was 111 kg/ha (Currah and Proctor, 1990). Thus, there are clearly enormous differences in average seed yields depending on genotype, locality, season and method of seed production.

Locations for seed production

Regions with reliably warm, dry summers are best for onion seed production. Low atmospheric humidity reduces the risk of diseases like downy mildew and purple blotch (see Chapter 5). Clear, bright, warm weather during flowering is favourable to a high activity from pollinating insects. In the USA, parts of Idaho and Oregon are climatically well suited for producing seed of the 'long-day' US varieties. 'Short-day' types are produced in the south-western USA, particularly the Imperial Valley of California (Jones and Mann, 1963). In northern Europe,

onion seed production is dominated by Dutch seed companies, who operate in southern Europe – particularly in Italy, southern France and Spain – because the warm, dry summers are well suited to the production of disease-free seed crops of onions (and leeks). Small-scale seed production for breeding purposes still occurs in cooler regions, and can be very satisfactory in polyethylene tunnels (Dowker *et al.*, 1985).

Methods of production

There are two basic systems of production: (i) bulb-to-seed production, in which a bulb crop is raised first and seeds are produced from the planted bulbs; and (ii) seed-to-seed production, in which growing plants are vernalized and induced to flower and produce seeds without going through a bulb stage. The former system has the advantage that it is possible to select the bulbs for maintaining the quality of the seed stock and to discard off-types – for example, double bulbs, misshapen bulbs or premature bolters (Peters, 1990). On the other hand, this method normally takes 2 years to produce a seed crop.

Seed-to-seed production is possible where the crop can overwinter as growing plants. It is important that vernalization is sufficient to induce 100% flowering, otherwise this method of production will result in the selection of easy-bolting genotypes. To ensure 100% bolting, seed is sown several weeks earlier than normal for a bulb crop, and irrigation is applied to ensure rapid emergence and quick growth to a post-juvenile size so that vernalization starts as the autumn begins (Jones and Mann, 1963). Heavy soils, with a high water content, create a slightly cooler microclimate and this is important for vernalization in warm regions like the Imperial Valley of California.

BULB-TO-SEED PRODUCTION

Raising mother bulbs

The first stage in the bulb-to-seed method is to raise mother bulbs. This is essentially the same as producing a normal bulb crop. Bulbs of 4–6 cm diameter are generally required. During growth of the crop, roguing for abnormal foliage, thick necks and uneven maturity can be carried out at the appropriate times.

Storage of mother bulbs

Autumn-sown cultivars are normally stored at ambient (often warm) temperatures after an early summer bulb harvest and planted in the autumn, after which they are vernalized by low temperatures in the field. In hot regions it may be necessary to vernalize bulbs by cold storage before planting: 90 days at 8–10°C was the optimal treatment for the Sao Francisco valley in Brazil, where the mean temperature of the coolest months is 27°C (Currah and Proctor, 1990). If cold storage before planting can be used, it is possible to ensure reliable flowering of seed crops in such regions, while avoiding using genotypes that bolt too easily when grown for bulbs. Mother bulbs of spring-sown cultivars are

usually vernalized by cool temperatures during storage, and they are planted out in spring. Storage temperatures between 4.5 and 14°C are suitable, with an optimum of about 11°C.

Planting mother bulbs

Bulbs are normally planted 10–15 cm deep in rows 50–100 cm apart. Closer inter-row spacing can give higher yields, but this increases the risk of attack by fungal disease. To minimize this risk, ventilation can be improved by orienting rows in the direction of the prevailing wind.

Seed yield increases with plant population. For example, in October-planted trials near Salerno, Italy, grown in rows 80 cm wide using bulbs with a mean weight of 100 g, seed yields increased linearly from about 700 to 1200 kg/ha when density increased from four to 12 bulbs/m^2. The number of umbels increased from 11 to 35/m^2, but seed weight per umbel declined from about 6.0 to 3.6 g (Cuocolo and Barbieri, 1988).

As mother bulb size increases, given a constant planting density, the yield of seeds increases, chiefly because the number of umbels per plant increases, and this more than outweighs a slight decrease in the weight of seeds per inflorescence. For example, Cuocolo (1989), using a population of 12.5 bulbs/m^2, found that seed yield increased linearly from about 1200 to 1800 g/m^2 as the median weight of the mother bulbs increased from 30 to 190 g, corresponding to an increase in planting rate from 3750 to 23,750 kg/ha. The mean number of umbels per plant increased linearly from about 2.7 to 5.0 over the same range of bulb size, whereas the mean weight of seed produced per umbel decreased from about 4.7 to 3.9 g.

The proportion and arrangement of pollinator and male-sterile mother bulbs planted is important in F_1 hybrid seed production (see Chapter 3). Ratios of fertile:sterile of 1:3 or 1:4 are used, frequently with two pollinator rows alternating with eight male-sterile rows (Currah, 1981).

Isolation of seed production fields

Because onions are easily cross-pollinated by insects from neighbouring fields, it is important to maintain varietal purity by separating the seed production of different cultivars. Similar cultivars should be kept at least 400 m apart, but seed fields of different-coloured cultivars should be 5 km apart (Jones and Mann, 1963). Male-sterile lines and their maintainers should be isolated by 5 km, or grown in insect-proof cages to prevent contamination by fertility-restoring pollen.

Irrigation and fertilizer

To maximize and to help stabilize yields, irrigation is important in most onion seed-producing regions (see Table 6.6). Irrigation can increase the risk of foliar disease if humidity is high, and furrow or drip irrigation is preferable to sprinklers to reduce this risk.

Field studies of flowering onion plants show that the lowest water potential (greatest water deficit or stress) is found in the individual flowers and pedicels

Table 6.6. Effect of irrigation on seed yield of late November-planted Yellow 'Sweet Spanish' onion grown at 11 plants/m^2 at Davis, California, USA (from MacGillivray, 1948).

Water applied (mm)	Number of irrigations	Seed yield (1944, kg/ha)	Seed yield (1945, kg/ha)
0	0	524	434
125	2	628	528
375	5	705	783
$LSD_{0.05}$	–	NS	217

NS, not significantly different.

of the umbel (Millar *et al.*, 1971). There is a particularly sharp decrease in water potential between the seed stalk and the umbel, indicating a high impedance to water flow in this region, possibly because the xylem divides into many small vessels to supply up to 1000 pedicels per umbel. Decreases in water potential from –4 to –15 bar between dawn and mid-day were measured in well-irrigated onion seed crops in Wisconsin, USA. Drought plus hot, dry winds, sometimes aggravated by root destruction by pink root disease (*Pyrenochaeta terrestris*), can lead to shrivelling and death of developing seeds at the 'milk' and 'dough' stages of endosperm development (Harrington, 1974).

Adequate nitrogen fertilization is essential for maximum yields. In Italy, where good yields (> 1000 kg/ha) are consistently produced without irrigation, the effects of a range of six N fertilizer levels – from 0 to 150 kg/ha in 30 kg/ha increments – was tested (Cuocolo and Barbieri, 1988). The nitrogen was applied as ammonium sulfate, one-third at planting in mid-October, one-third in late January and one-third in late March (seeds were harvested in July). Seed yield increased linearly from 830 to 1100 kg/ha with increasing N. Nitrogen and water requirements are interrelated: higher N is needed where rainfall or irrigation make high yields possible.

The synchronization of flowering

It is important when producing F_1 hybrid seed that the male-fertile and male-sterile lines flower simultaneously. There should always be plenty of pollen from the male-fertile line available while stigmas of the male-sterile mother plants are receptive, thereby minimizing the risk of contamination from pollen of other lines carried by visiting insects, or from the occasional male-fertile mother plant. The different lines of a hybrid do not necessarily bloom simultaneously when treated identically. Techniques to overcome this problem include: (i) storing bulbs of the two lines at different temperatures before planting – the closer the temperature during storage to the optimum for inflorescence development (usually around 10–12°C) the earlier the inflorescence emerges after planting out; (ii) staggering the planting dates of the two lines – the earlier the planting date the earlier

inflorescences tend to appear; and (iii) growing one line from autumn-sown seeds and the other from mother bulbs. An autumn-sown crop grown from seed will normally bloom later than the same line grown from mother bulbs.

Seed stalk disease and seed infection

Fungal diseases, which tend to spread in conditions of high humidity when there are prolonged periods of plant surface wetness (see Chapter 5), are potentially very serious in seed crops. The developing seed stalk can be completely girdled and destroyed by such infections. Probably the most serious disease in onion seed production is downy mildew, *Peronospora destructor*. In addition to the use of fungicides, many of the cultural practices of growing onion seed crops – for example, fairly wide row spacings and limited autumn applications of N fertilizers to avoid excessive leaf growth – are aimed at maintaining good ventilation within the crop, thereby making the conditions less conducive to the spread of downy mildew (Peters, 1990). Purple blotch – *Alternaria porri*, *Stemphylium vesicarium* and various *Botrytis*, particularly *B. squamosa* – also cause serious damage.

Pollination

Experiments in which onion umbels were bagged have established that very little pollination was accomplished without access by insects; wind and gravity being of little importance. From tens to hundreds of different species of insect have been identified visiting blooming onion umbels, the number of species depending on the locality (Currah, 1990). Honeybees are the most important, and seed producers hire hives of bees and site them in the onion fields during flowering. In the USA, between 12 and 37 hives/ha are used. The introduction of the beehives is staggered in time, starting from when about 50% of umbels are showing some open florets. After some days the bees may learn to forage on more attractive neighbouring crops, so by staggering their introduction their initial 'naive' behaviour, when they tend to stay on the onion flowers, is exploited. Bees forage for nectar, not pollen, from onion flowers, and they are active at air temperatures above 16°C. They move more frequently from umbel to umbel when the sky is clear and cloud free, therefore increasing the chances of cross-pollination in sunny weather.

In the USA, onion pollen appears to have decreased in its attractiveness to honeybees over the years. The reasons for this change are not fully understood, but may be due to high levels of potassium in the nectar of hybrid onions. Very high sugar concentrations (> 50%) can occur in onion nectar, and this also makes it unattractive to bees. To attract bees onions must produce abundant nectar and, when inbreeding to produce male-sterile lines, it is essential to ensure that the ability to produce nectar does not disappear; such lines are useless for seed production.

Pollen fertility varies with temperature. At 14°C pollen abundance and viability is low, but is higher at 23°C. Male sterility tends to break down at high

temperatures, and male-sterile lines should be selected under high temperatures. When producing hybrid seed, male-sterile lines must be rogued for male-fertiles during blooming, and these must be destroyed to prevent pollen contamination. Pollen tube growth and seed set are adversely affected by temperatures above 40°C. Temperatures 20°C above ambient air temperatures have been recorded in densely packed onion umbels in strong insolation with a low wind speed. A circular area of aborted flowers on the insolated side of the umbel, which can occur in these conditions, is termed 'dollar spot' in the USA. Ovary wall temperatures of 52°C give near 100% seed abortion, and such excessive temperatures are sometimes responsible for seed crop failures in the USA.

Seed ripening, harvesting and storage

The rate of progress towards seed ripening increases with temperature, and about 600 degree-days above 10°C are needed to progress from anthesis to the stage when ripe, black seeds start to be shed from the capsules. At seed ripening, seeds have attained their full dry weight and seed and umbel moisture content decline quite rapidly. Harvest must be timed just before the capsules start to shatter and lose seeds (see Fig. 6.17).

Seeds are hand-harvested when 25–30% of the umbels show ripe seed due to dehiscence of the capsules. Umbels are cut with about 15 cm of scape attached. To avoid seed losses, mechanized harvesting is best about 10 days earlier, when ripe seed can be seen on just 2% of the umbels and when the seed moisture content is 30–40%. After harvest the umbels may be dried in a variety of ways. In sunny climates they may be dried outdoors on plastic sheeting, in layers about 20 cm thick. The umbels should be turned regularly to avoid

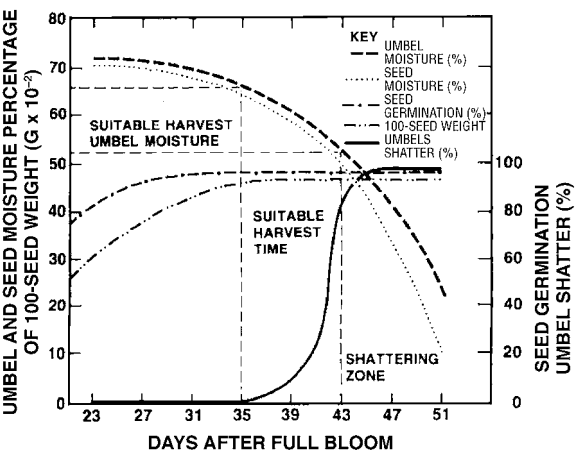

Fig. 6.17. The growth, drying and development of germinability of onion seeds on ripening umbels in relation to umbel shattering, harvesting time and seed quality (from Steiner and Akintobi, 1986. Courtesy of *HortScience*).

rotting and overheating. In moister climates the umbels are dried in bins under a warm air draught but, to avoid damage, the temperature of the draught should not exceed 32°C until the seed moisture content is less than 18%, 38°C until less than 10% or 43°C when below 10%.

When the umbels can be crumbled in the hand they are ready for mechanical threshing and cleaning. Seed should not be too dry at threshing otherwise the seedcoats are liable to be cracked, and this results in lowered germination. The trash can be separated from the cleaned seed by sinking the onion seeds in water and floating off the trash. After this, seed must be rapidly re-dried by centrifuging and drying under a forced draught to less than 12% moisture.

The principles underlying seed storage in order to maintain viability for a long period are described in Chapter 4. Low moisture content, low storage temperature and a high initial viability result in a long storage life. At high temperature and humidity onion seed loses viability faster than most vegetable seeds, and this is a serious problem in tropical areas. Commercially, seed is dried to about 6.3% moisture content and sealed into moisture-proof cans or foil packets. In these conditions it can remain fully viable for at least 3 years, even at warm temperatures, and can therefore be safely marketed to tropical areas. For long-term seed preservation in gene banks it is recommended that seeds are stored at 5% moisture content and −18°C, and are regenerated when the seedlot viability declines below 85% (Astley, 1990).

GARLIC PRODUCTION

The agronomy of garlic has been reviewed by Brewster and Rabinowitch (1990), Burba (1993) and Messiaen *et al.* (1993). Garlic is most commonly grown as an overwintered crop using strains locally adapted to produce high-quality bulbs following barn storage at ambient temperatures. Bulbs are separated into cloves just before planting. Cloves used for planting vary in weight from 1 to 9 g, with 4–5 g being common. Plant size and final bulb weight tend to increase with clove weight at planting. Cloves are planted with their bases 2–3 cm deep, usually at a density of around 40 plants/m^2 when grown with irrigation. The optimum plant density for producing the large bulbs that obtain premium prices depends on the potential yield. For rainfed crops that yield about 15 t/ha at the highest densities tested, a plant density of 14–18 plants/m^2 was found optimal for good-quality bulbs (Castillo *et al.*, 1996). However, bulb yields in fertigation trials in Mexico approached 40 t/ha at high plant densities and, in these conditions, 30–42 plants/m^2 was economically optimal (Castellanos *et al.*, 2004). Higher final yields may occur at higher plant densities, but bulbs may become too small. In California densities of 60/m^2 are used to produce high-yielding processing crops, when bulb size is unimportant.

Well-drained soils should be used, since cloddy soils create difficulties with mechanical harvesting. Phosphate fertilizer is frequently applied as a band

below and to the side of the cloves at planting. Nitrogen fertilizer applications are usually split, typically 50% at planting, followed by a spring application to the growing plants. The nitrogen in plant dry matter needed for maximum yield declines from about 6% soon after emergence to 1.5% near to harvest time. Like onion, garlic is a shallow-rooted crop. To attain maximum yields, moisture in the top 30 cm of soil should be maintained close to field capacity for most of the growing season. In California and in Israel it is recommended that irrigation ceases when pseudostems soften and the foliage falls, which is about 3 weeks before harvest. Irrigation later than this can result in rotting and skin discoloration.

When ready for harvest the roots are severed with an undercutting knife. In warm, dry climates the bulbs may then be left to dry in windrows in the field. Bulbs should be protected from sun-scald by shading them with the remains of the foliage. Dried tops and roots are then removed from the bulbs and they can be stored in sacks or ventilated bins to a depth of 2 m (see Chapter 7). Where rain or dew is heavy at the time of harvest, bulbs must be cured indoors. Modified potato harvesting machines can be used to mechanize harvesting. Mechanical topping and harvesting is satisfactory for garlic destined for processing.

LEEK PRODUCTION

Leek agronomy has been reviewed by de Clerq and van Bockstaele (2002). Leeks must be grown to a certain size before they are marketable. The criteria for marketability vary from outlet to outlet, and various specifications for marketable size have been used in scientific studies on the crop. Currently, leeks of pseudostem diameter greater than 20 mm and length greater than 150 mm, including a 50 mm 'flag' of green leaf at the top, meet UK supermarket specifications. Such leeks should have an average fresh weight of about 160 g.

In some past studies, all leeks of diameter greater than 12.5 mm have been classed as marketable, and in some more traditional markets large leeks, greater than 40 mm diameter, are required. In fact, the leek is a variable crop and some grading into different sizes is essential to satisfy the requirements for uniformity demanded by most outlets. In Belgium, leeks are frequently earthed-up as they grow to produce long, blanched, white pseudostems. In common with other vegetables, a market for small 'baby' leeks has developed in European supermarkets. Ninety per cent of leeks are sold for the fresh market in Europe, 10% for processing.

Cultural systems aim to produce high yields of marketable specification at the right harvest date. To achieve this, the grower has the choice of direct-drilled or transplanted crops, they can vary planting or sowing date, transplant size, plant density and cultivar and, for early production, they have the option of using plastic crop covers to advance growth. The leek is a hardy crop and in the cool, moist winters of western Europe, where temperatures rarely dip to –10°C,

it can stand in the field and be harvested throughout the winter. Crop storage for 2–4 months, depending on storage facilities, is feasible (see Chapter 7), and can be used to supply the market when fresh standing crops are not available.

Transplants

Various systems of transplant production are used, including bare root transplants, peat blocks and modular trays containing about 15 ml of compost per cell. Blocks and modules may be multi-seeded for planting as two- or three-seedling clusters. The production regime is similar to that for onion (see above). Typically, 18°C will be applied for the first 3 weeks from sowing, followed by 14°C, with 10°C for a week or two before planting to harden the plants. Seedlings are slow growing and plant-raising usually takes 8–12 weeks, depending on light and temperature (see 'Leeks, growth and development' in Chapter 4) and the size of transplant required.

In UK trials, seedlings sown in 27 mm peat blocks on 20 January reached the same weight by 29 March (0.45 g) as seedlings sown 3 weeks earlier into 15 ml cells in modular trays, so rooting volume and medium can be important. The longer the seedlings are growing before planting, especially if exposed to low temperature, the sooner the leeks bolt (see Fig. 4.52), so treatments that promote rapid growth to transplanting size are preferable.

Yields and mean plant weights at harvest correlate well with mean weight at transplanting. For example, Benjamin (1984) raised seedlings in peat blocks from a 30 March sowing and 7 weeks later graded them into large, medium and small sizes, which had mean fresh weights of 0.619, 0.451 and 0.214 g, respectively, and planted them in separate plots. At harvest, 221 days later, the corresponding mean plant weights were 299, 261 and 217g. Therefore, for early production, large seedlings are preferable. Also, the yield of maincrop leeks decreases as planting is delayed from May onwards (see Fig. 4.50 and Table 4.7). To compensate, the Dutch recommend planting seedlings of 3.0–3.5 mm diameter in May, but of 5–6 mm in July.

Leeks are commonly planted on a bed system, typically in rows about 30 cm apart. If they are to be earthed-up during growth they may be planted in the base of furrows. In the UK, a typical transplanted maincrop would be sown in mid-March, transplanted at about 40 plants/m^2 in early June, given a basal fertilizer application of 130:60:160 kg/ha of N:P:K, followed by an additional application of 150 kg/ha of N in mid-August and irrigated during dry periods. Residual herbicides are applied to the beds, and pesticides to control thrips and leek rust are usually necessary (see Chapter 5). Under such a regime in variety trials at Luddington, central England, mean total yields and yields of leeks greater than 25 mm diameter were, respectively (in t/ha) 30.2 and 19.3 on 29 September, 40 and 33.5 on 24 November and 40 and 34 on 2 February. By 7 May 78% of the plants were visibly bolting and therefore unmarketable.

Direct sowing

The crop can be established more cheaply than transplanting by direct sowing into beds in the spring. The viability and vigour of leek seed is highly variable, and high-quality seed is important for direct sowing (see Chapter 4). The majority of leek seed sold in the UK is now primed using the 'drum' method (see 'Seed Priming', above). Besides being cheaper, direct sowing tends to result in crops with less dirt in the leaf axils and with fewer bent pseudostems, but the length of blanched sheath tends to be shorter than with transplanted crops, and direct-sown crops are more prone to bulbiness (Williams, 1973).

Plant density

The optimum plant density for leeks depends on the size grade required at harvest, the date of planting or sowing – which influences the potential yield (see Figs 4.50 and 4.51) – and the intended harvest date. Mean width and length increase as the crop grows, and increase as plant density decreases. For leeks of 20 mm minimum diameter and 150 mm minimum length, a planting density of about 30 plants/m^2 is optimal for early production, e.g. for late-June harvesting following a late March or early April transplanting of mid-January-sown modules.

Trials in the UK with leeks sown directly into beds at the end of March, which were thinned to densities of 20, 42, 84 and 126/m^2, showed that percentage survival decreased with time and as density increased. Mortality was almost 50% by mid-January from the two highest-planting densities, but only 10% at the lowest density. Yields reached a maximum in about mid-November, and the highest yields of marketable leeks (> 12.5 mm diameter) occurred with 50–60 plants/m^2 at harvest. At this density a yield of 44 t/ha of trimmed leeks was produced from a total crop fresh yield of 107 t/ha. Yields were lower from both a mid-September and a mid-January harvest, with marketable yields at 29 and 34 t/ha, respectively. Optimum densities for the early and the late harvest, at about 40 plants/m^2, were slightly lower than for the November harvest, when the crop was at its peak yield (Williams, 1973).

The higher the plant density, the higher the proportion of undersized, unmarketable leeks but, up to an optimum density, this is outweighed by the larger total number of plants from high densities. However, to produce large leeks, densities of 15–25 plants/m^2 are used. Leeks grown at a high plant density appear more elongated than those grown at low density, i.e. the pseudostems have a higher length:breadth ratio. Also, the degree of blanching increases with density, especially for plants from the centre of beds.

Variability

One of the main problems with leek production is the great plant-to-plant variation in the crop. In both transplanted and drilled crops the coefficient of variation in shoot weight at harvest is typically 50–70%. With modern market outlets requiring uniform grades, e.g. for supermarket pre-packs, variability results in much work grading the crop after harvest, as well as wastage of plants that are under- or oversized. In a drilled crop, 25% of the variability at an early harvest was attributable to differences in the timing of seedling emergence, and in a transplanted crop 15% was attributable to plant size soon after emergence.

In another experiment on a crop directly sown in late March, the coefficient of variation of plant weight was 74% in late September and 59% in February. At these two harvest dates, respectively, 47.6 and 19.7% of the variability could be accounted for by differences in timing of seedling emergence, seed size, sowing depth and distance to neighbouring plant or row, all of which were recorded for individual plants. Of this, only about 7% of variability could be attributed to seed size or sowing depth differences (Benjamin, 1984). The use of primed seed reduces the variability associated with differences in the time of seedling emergence in drilled crops. Variability tends to increase with plant density, in common with most vegetable crops. In one experiment coefficients of variation at harvest were 61% at 50 and 44% at 22 plants/m^2. The increased plant competition at high densities accentuates any differences in plant size already established.

These studies have shown that plant-to-plant differences during crop establishment account for a much lower proportion of variability at harvest than is the case with other vegetable crops. For example, with lettuce and carrot, about 50% of variability at harvest is attributable to differences in time of, or size at, emergence. Therefore, with leek, differences in growth rate after establishment are more important than for other crops, probably because of inherent genetic variability within leeks (see Chapter 3). By selecting for uniformly large seedlings at transplanting, the coefficient of variation was reduced to 28% at harvest 220 days later, whereas medium and small plants at transplanting gave coefficients of 39 and 57%, respectively, and the unselected population 49% (Benjamin, 1984). In this way, genotypes with more uniform growth rate may be selectable at transplanting, but at the cost of raising many reject seedlings. Seedling size at transplanting shows a good correlation with weight and thickness at harvest time (de Clerq and van Bockstaele, 2002).

There can be up to 20% self-fertilization in leek seed crops, and yields from selfed seed range from 26 to 80% less than from cross-pollinated seed. Thus selfing is a major source of the variation within a leek seedlot. Some of this variability will be eliminated when weak seedlings are discarded in transplanted crops. However, hybrid leeks, based on male sterility, eliminate the problem of selfs and give greater uniformity of seedlings and at harvest (de Clerq and van Bockstaele, 2002).

Plastic mulches for early cropping

Bolting in spring curtails the period of marketability of overwintered leek crops. In the UK there is then a gap of about 3 months before spring-planted crops reach marketable size. Storage of harvested leeks can help maintain supplies during this gap (see Chapter 7), but also early harvests can be advanced by using transparent crop covers. Trials show that mulches of polyethylene film with 500 perforations of 1 cm diameter/m^2, or with non-woven polypropylene fabrics, can advance harvests. The films are laid over the crop at transplanting, which is usually in late March or early April, following a January sowing in glasshouses. As the crop grows these light films are raised by the foliage, and 'float' on top of the canopy of leaves. Rainfall penetrates the perforations. Mean temperatures are raised by 1–2°C under these mulches, resulting in faster growth. The mulches are removed about 7 weeks after transplanting. This is particularly important if the weather becomes hot.

For early production it is important to use quick-growing, long-pseudo-stemmed cultivars, which rapidly reach marketable length. Densities of about 30 plants/m^2 are optimal, and herbicide and base fertilizer treatments are similar to those for open-grown crops. Two N top-dressings using 50–100 kg/ha N should be applied to maintain an unrestricted growth. Leeks are slightly elongated by growing under such mulches, and bolting can be slightly delayed. In UK conditions marketable yields of 14 t/ha were achieved by late June, and 31–40 t/ha by late July, with an advancement of 7–9 days over the unprotected crop. Imports from southern Europe also help fill the supply gap in May and June in northern Europe.

Leek seed production

The quality of leek seed – as shown by its germinability, rate of germination and emergence percentage in field conditions – is highly variable. In a survey of 23 commercial seedlots, Gray and Steckel (1986) reported that 50% of them had below 80% germination and several were as low as 50–60%. Without high-quality seed, it is impossible to establish the required plant population in directly drilled crops. Also, the high costs of modular transplant production make it important that empty modules, caused by non-viable seeds, are few. These considerations have motivated research into the factors influencing seed quality in leeks and into methods for producing high-quality seed.

Traditional production methods

Traditionally, leek seed is produced from stecklings (shoots with most of the foliage trimmed off) planted in the autumn at 5–17 plants/m^2, which flower outside in the following year. Seed heads are cut in the autumn and dried in stores, ensuring that aeration is sufficient to prevent rotting. After drying, the

seedheads are threshed and the seed cleaned. Yields of 0.6–0.9 t/ha are typical (Bonnet, 1976). Compared with onion, leek seedheads are slow to develop, and it takes approximately 50% longer in terms of day-degrees (> 6°C) after flowering for leek seeds to reach ripeness (Gray and Ward, 1987). Consequently, seedheads are often harvested in late autumn after the onset of damp weather, and this may contribute to the poor quality of many seedlots.

Production in polyethylene tunnels

Trials in the UK have shown that 1.5–2.5 t/ha of seed with about 90% germination can be produced consistently from year to year in polyethylene tunnels (Gray *et al.*, 1991b). The production method involves sowing for steckling production in June, followed by the transplanting of 1.0–1.5 cm-diameter stecklings, at 50–60 plants/m^2, to tunnels in mid-winter or early spring with basal N, P and K levels of 72, 224 and 224 kg/ha. To avoid wetting the foliage, trickle irrigation is used. Flowering usually occurs over 5–6 weeks, starting in mid-June, and during this time blowflies are introduced and replenished weekly using about 3.4 l of blowfly pupae/100 m^2 of tunnel area. The optimum time for harvesting is when the seeds have blackened but before the capsules open and start to lose seeds by shedding. At this stage the seed still has a moisture content of about 60% (see Fig. 6.18b).

Provided seed is left to dry and ripen within the capsule, high-quality seed results even though seedheads are harvested at an immature stage. Seed growth and the development of germinability continue after harvesting of the

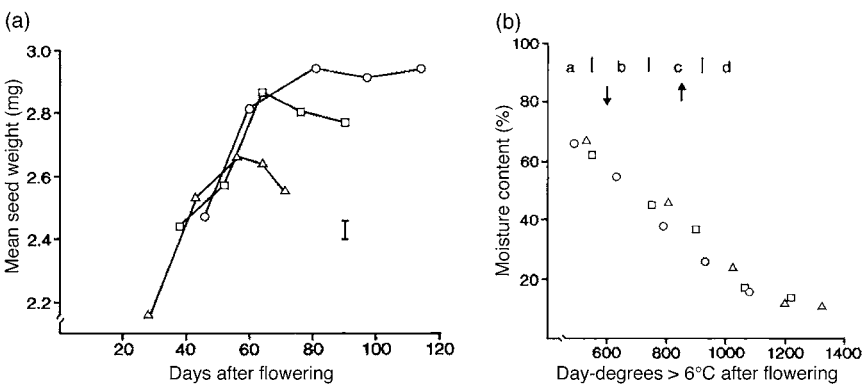

Fig. 6.18. (a) Change in mean leek seed dry weight with time at 20/10 (○), 25/15 (□) and 30/20°C (△) day/night. Data are averages of 3 years of experiment; vertical bar = LSD (P = 0.05). (b) Loss of seed moisture content during development of leek *versus* day-degrees > 6°C after flowering. Key: ↓, majority of seeds black; ↑, capsule splits; a, endosperm milky; b, 'soft cheese' endosperm; c, 'hard cheese'; d, flint hard. Standard error less than symbol size (from Gray *et al.*, 1992. Courtesy of Seed Science Research).

seedheads (Gray *et al.*, 1992). Unlike onion, seed moisture content is not a reliable guide as to when to harvest. Normally, the seedheads are harvested with 15–30 cm of stalk attached and placed to dry at 20–35°C for 4–6 weeks. After this, the seedheads can be threshed, the seed extracted and cleaned and stored at low temperature and humidity, as for onion (see above).

Seed dormancy and size

Leek seeds sometimes show high-temperature dormancy, with slow and low germination at temperatures > 20°C from seedlots that have good germinability at lower temperatures. This occurs when seedheads develop at cool temperatures (e.g. 15°C) and is avoided if seedheads develop and dry at mean temperatures of 20°C or above (Gray *et al.*, 1992). Smaller seeds are formed when seedheads ripen at warm rather than at cool temperatures, because the duration of seed growth is shorter at warm temperatures (see Fig. 6.18a). There is no general correlation between seed viability and seed size, but a correlation between seed weight and transplant size has been demonstrated (de Clerq and van Bockstaele, 2002).

JAPANESE BUNCHING ONION PRODUCTION

The culture of these onions is described by Inden and Asahira (1990), and by Larkcom (1991). They are sold in various forms: (i) as small, green bunching onions; (ii) as green shoots 40–90 cm long with tender, green leaves plus one-quarter to one-third of the length as white pseudostem; and (iii) as long, blanched pseudostems, similar in appearance to the large leeks of Europe. By harvest time the green leaves on the latter types tend to be tough, and are discarded.

Cultivars for blanched pseudostem production do not branch freely and fall within the 'Kaga' and 'Senju' groups according to their winter hardiness and growth rate at cool temperatures (see Chapter 1). The hardy types, which survive over winter in cold regions, grow slowly at low temperatures (see Chapter 1). Types for green shoot production branch more freely and predominate in the 'Kujyo' group. Green shoots may be harvested any time from 40 days to 12 months after sowing, depending on size at harvest and time of year. Early spring growth is often accelerated by using polythene tunnels.

For blanched pseudostem production in Japan, seeds are spring-sown for harvest the following winter, or autumn-sown and spring-transplanted for summer, autumn and winter harvest. The seedlings are transplanted into furrows about 15 cm deep with about 9 cm between plants in the row. Three or four times during growth, earth is pulled round the pseudostems so that ultimately they are growing in earthed-up ridges. Fertilizers are applied three or four times during the growing season, typically applying totals of 200, 150 and 175 kg/ha of N, P and K, respectively. The harvested pseudostems vary in length and thickness, but can be up to 50 cm long and 3.5 cm wide.

CHIVE PRODUCTION

In Germany, chives are grown for fresh shoots as a winter glasshouse crop, following the breaking of dormancy by heat treatment (see Chapter 4). In Denmark and in New Zealand they are grown as a field crop for drying or freeze-drying. In Denmark, seeds are sown in April or May in double rows 5 cm apart, with 50–65 cm between the twin rows. In the first season not more than three cuts of leaves are made. The crop is perennial, and in subsequent seasons six to seven cuts are harvested. Cuts made during the flowering period of late May and June are discarded, since the flower stalks are tough. Cutting ceases in September to allow the plants to accumulate reserves for overwintering. Irrigation is essential to avoid formation of dead and yellow leaves. Annual yields of about 7.5 t/ha of fresh leaves are taken in Denmark (Poulsen, 1990).

CHINESE CHIVES PRODUCTION

This crop is popular in China and Japan, and is becoming better known as a gourmet vegetable elsewhere. Its cultivation is described by Larkcom (1991). It is grown as a perennial crop for leafy shoots, harvested both green and blanched, and for its edible flowers. New crops can be raised from seed, and seedlings are frequently transplanted as clusters of ten or so, spaced 20 cm apart in rows that are themselves 30–40 cm apart.

In the first season of growth, to encourage deep rooting, irrigation is applied only if the leaves start to die back with drought. Any flower stalks are cut and prevented from development in the first season, to encourage the build-up of the rhizomes. Cutting starts in the second season when the leaves are about 20 cm long. The number of cuts per year varies from about four in northern China to eight in the south of the country. After each cut, a liquid feed with nitrogenous fertilizer is recommended. To produce blanched shoots the plants are blacked-out following a leaf cutting, using black polythene tunnels or more traditional materials like clay pots or thatch. To avoid weakening the plants, no more than one cut of blanched shoots should be taken in succession. In the spring, before growth starts, the beds should be raked to remove leaf debris and the soil should be earthed-up round the plants, or applied as a 4–5 cm layer to the beds, to counteract the tendency of the rhizomes to get nearer the surface with time. In cold regions, winter and early spring growth can be achieved using greenhouses and polythene tunnels.

The edible flower stalks are cut when 30–40 cm long while the flower buds are still green. In Japan, early-flowering types with tender flower stalks have been developed especially for edible flower production. Both the leaves, particularly when blanched, and the flowers are highly perishable and should be marketed quickly and kept cool during transport and selling (see Chapter 7).

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7

Crop Storage and Dormancy

The edible alliums range from some of the most highly perishable vegetables to the most long-storing. Some shallot strains probably represent the extreme of storability, while the delicate green shoots of Chinese chives – which can be stored for just 2–3 days, even at 0–2°C (Saito, 1990) – represent the extreme of perishability. The bulb-forming crops – onion, shallot, garlic and rakkyo, which develop dormant bulbs in response to long photoperiods and high temperatures – are, by nature, suited to storage. Allium crops harvested as fresh shoots, i.e. leeks, salad onions, Japanese bunching onions, chives and Chinese chives, are not harvested in a dormant state, and so their storage life is shorter and the conditions they require are similar to those for other leafy vegetables. Winter dormancy, typical of many temperate vegetative plants, is found in many of these leafy crop species, e.g. in chives (see Chapter 4) and in cultivars of Japanese bunching onion and of Chinese chive adapted to regions with cold winters.

However, winter dormancy involves the die-back of leafy shoots, and these crops are not harvested while dormant. Most of this chapter is concerned with the dormancy and storage of onion bulbs, this being both interesting physiologically and the most economically important aspect of allium storage. Garlic dormancy and storage, which has close parallels with onion, is then considered. Finally, and as a contrast, the storage of leeks and salad onions is described.

BULB CROP STORAGE AND DORMANCY

The bulbs of edible alliums are naturally dormant organs adapted to maintaining the plant's viability during a period unfavourable for growth. In the native habitat of the wild ancestors of onions and garlic, the bulbs may have enabled the plants to survive periods of summer drought and winter cold. Rational bulb storage rests on knowledge of the physiology of bulb dormancy and the pathology of diseases of stored bulbs (see Chapter 5). Numerous studies have investigated physiological aspects of dormancy in onion bulbs, and rather fewer have studied this topic in garlic. There have also been many agronomic studies investigating the influence of various cultural practices and storage

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regimes on storage life but the causes of loss, whether by rotting due to disease or sprouting, were not always distinguished. Reviews on these topics were published by Komochi (1990), Gubb and MacTavish (2002) and Chope (2006), and these authors provide extensive bibliographies of the research literature.

The physiology of dormancy in onions

Bulb development and structure in relation to dormancy

Many fundamental aspects of what is known about onion dormancy were discovered or elegantly demonstrated by Abdalla and Mann (1963). They followed bulb development, rest and sprouting in cv. 'Excel', a cultivar with innately short dormancy, grown in the field at Davis, California, USA. During growth, leaves were initiated at the shoot apex at a rate of about one per week (see Fig. 7.1).

Leaves initially differentiated into bladed leaves, and later, as bulbing commenced, into three or four bladeless storage leaves (bulb-scales) (see Fig. 4.26). Within these were formed five or six non-elongated leaf initials that again had blades, and which later formed the shoots that sprouted from the bulb; these are termed the 'sprout leaf' initials. Leaf initiation at the shoot apex ceased about 20 days before bulb harvest (see Fig. 7.1), while the leaves were still green and erect. Root initiation ceased at about the same time. Leaf initiation resumed within stored bulbs about 2 weeks after harvest.

Cell division at the shoot apex continued right up to harvest and then declined after curing, to remain at a low level during storage. Sprout elongation within the bulb during storage was due to the elongation of pre-existing cells in the 'sprout leaf' initials that were formed late in bulb growth and was not,

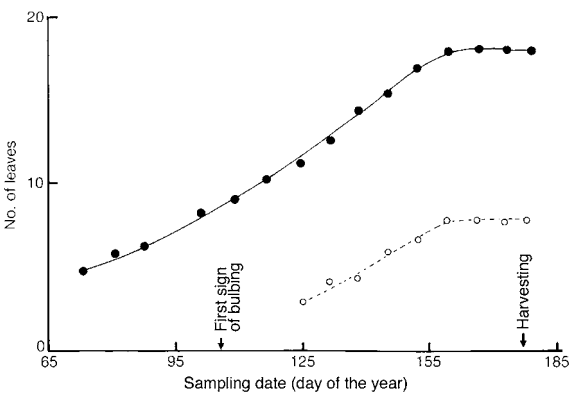


Fig. 7.1. Leaf initiation on the main axis (solid line) and first axillary bud (broken line) of onion cv. 'Excel' sown on 31 December at Davis, California, USA. The first eight to nine leaves were bladed, the next three to four were bladeless bulb scales and the last five to six were bladed sprout leaf primordia (see Chapter 2) (from Abdalla and Mann, 1963. Courtesy of *Hilgardia*).

therefore, dependent on cell division at the shoot apex. More recent studies have shown the same sharp decline in cell division at the shoot apex at bulb maturity in northern European cultivars, as indicated by the low proportion of cells in mitosis (see Fig. 7.2a) (Pak *et al.*, 1995). Cell division resumed within 2–4 weeks of harvest. The messenger RNA needed to produce histone 2A, a protein incorporated in chromosomes at mitosis and therefore associated with this cell division, has also been shown to decline sharply in shoot apices at bulb maturity and to begin to increase after harvest (see Fig. 7.2b; Carter *et al.*, 1999).

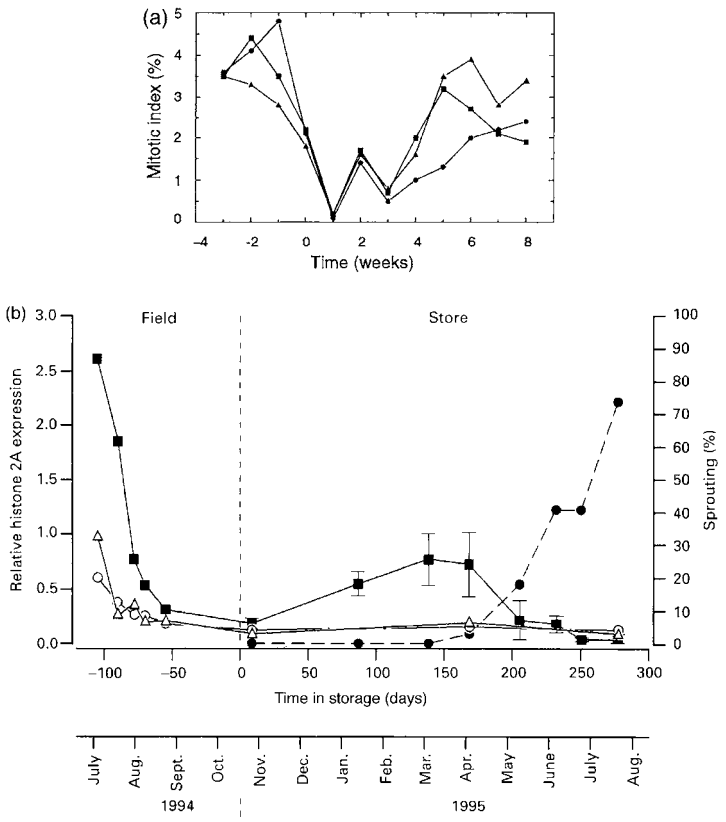


Fig. 7.2. (a) Cell division in the shoot apex meristem of bulbs of onion cvs 'Hysam' (●), 'Hystar' (■) and 'Centurion' (▲) shown as the percentage of dividing cells (the mitotic index) starting 3 weeks before harvest (harvest was time 0) and during subsequent storage at 16°C. Values are means of five apices (from Pak *et al.*, 1995. Courtesy of *Physiologia Plantarum*). (b) The relative expression of the messenger RNA specifying the protein histone 2A that is necessary for cell division in the inner bulb, which includes the shoot apex (■) in the middle bulb (○) and the outer bulb (△) of onion cv. 'Robusta' during bulb formation and subsequent storage. The bars around the values for the inner bulb are standard errors of the mean based on three determinations from three replicate bulbs. Percentage visible sprouting is shown as ● (from Carter *et al.*, 1999. Courtesy of *New Phytologist*©, 1999).

The peak of histone synthesis associated with a peak of cell division in the shoot apex of stored bulbs occurred at about the same time (150 days after harvest) in cultivars that visibly sprouted at that time or in those that took a further 100 days to visibly sprout (Carter *et al.*, 1999). So, sprouting time was not necessarily associated with cell division at the shoot apex, since the interval between this meristematic activity and the elongation of the sprout leaves differed between cultivars.

There has been some debate as to what constitutes dormancy in onion bulbs, since metabolic changes continue through the period from bulb maturity to sprouting (Gubb and MacTavish, 2002). An absence of visible growth has been proposed as a clear-cut criterion for dormancy, and a method to determine whether sprout leaves have started elongating has been devised (Bufler, 2001; Yasin and Bufler, 2007; Bufler, in press, a). The technique is based on the observation that the blades of sprout leaves elongate well before a slow elongation of the sheath. The initial mean and standard deviation of leaf blade length in sprout leaves with sheath lengths in the range 2.0–3.5 mm dissected from bulbs following harvest and a 2-week curing are used to define sprout leaf blade length in dormant bulbs. In subsequent samples, sprout leaves with sheaths in the range 2.0–3.5 mm are measured, and those with leaf blades longer than the mean value for dormant bulbs, plus its 95% confidence interval, are assumed to have started elongating and, therefore, to be sprouting and to have exited dormancy.

There is variation in the time to commencement of sprout leaf elongation between individual bulbs within a cultivar, and hence to get a clear picture of metabolic changes occurring at the shoot apex of bulbs as they emerge from dormancy it is important to make measurements on sprout leaves and their enclosed apices from individual bulbs, not on samples bulked from several bulbs (Bufler, in press, a; Yasin and Bufler, 2007).

The skin of onion bulbs

The skin of an onion is the first thing a potential purchaser sees, and attractive, intact skins are essential for high-quality onions. Therefore, knowledge of how to produce and maintain sound and attractive skins is important for the onion industry. The outer, dry skin of the onion bulb protects the inner, fleshy scales from damage and disease, and prevents them drying out. During the maturation of bulbs the outer scales lose water and form thin, dry skins that completely envelop the bulb. Chemical changes to the flavonoid pigments occur during skin drying, and these determine the final external colour of the bulbs, which is important in many markets. Also, phenolic substances formed in this process make skins resistant to invasion by microbial pathogens.

Changes in the structural carbohydrate composition, as fleshy skins dry to form papery scales, give rise to greater strength and the water-absorbing properties of the outer scales. Skin flexibility versus brittleness, and also the permeability to water, vary with skin water content. These physical properties influence the resistance of skins to damage and loss during handling, and also the rate of water

loss from bulbs. Skins split and slough off if onion bulbs are handled roughly at harvest or during removal from storage, grading and delivery to market.

There may be between one and three dry skins on an onion depending on conditions. These are 0.02–0.10 mm thick depending on variety and position on the bulb (Tanaka *et al.*, 1985c; Tanaka, 1991; Hole *et al.*, 2002). The skins are thinnest at the widest part of the bulb and on the side of the bulb opposite to the former leaf blade. The dry skins consist of tightly compact layers of cells with a shiny outer cuticle.

THE CURING OF BULB SKINS As bulbs ripen before and after harvest, the drying of the outer scales is accompanied by biochemical changes that give rise to dark pigments and antifungal substances in the dry skins and to changes in structural carbohydrate composition of the cell walls; this is the process of curing. It is known that temperatures > 21°C and high humidity round the bulbs during curing promote a dark-coloured skin (Isenberg and Ang, 1963). In bulk stores it has been found that the depth of colour in onion skins corresponds to the number of day-degrees above a base of 21°C that the onions receive during curing (Bleasdale *et al.*, 1970). Warmth might favour rapidity in the reactions leading to browning, and high humidity may slow drying out and therefore prolong the period during which both the enzymic and auto-oxidative reactions described next can occur.

During the cell senescence and drying of onion outer scales as they are curing, di- and mono-glucosides of quercetin (see Fig. 8.9) are converted to free quercetin by glucosidase enzymes, particularly in the still moist but drying areas of the scale. In this zone the level of the enzyme peroxidase is high, and this can oxidize free, but not glucoside-linked, quercetin to produce 3,4-dihydroxybenzoic acid (protocatechuic acid) and 2,4,6-trihydroxybenzoic acid in reactions involving hydrogen peroxide (Takahama and Hirota, 2000). The hydrogen peroxide formed in the senescing cells, coupled with the decrease in ascorbic acid (vitamin C) that occurs in ageing onion scales, are probably factors favouring the peroxidase-dependent oxidation of quercetin to phenols like 3, 4-dihydroxybenzoic acid. In non-senescent tissue, ascorbic acid counteracts the oxidizing action of hydrogen peroxide. In the presence of hydrogen peroxide, the phenolic substances can undergo further autooxidation reactions to form quinones and hydroquinones, and these can participate in cross-linking reactions to form dark-coloured polymers, the exact structures of which are not yet known (Takahama, 2004). This process is similar to lignin formation.

Protocatechuic acid has long been known to confer resistance to the onion smudge fungus, *Colletotrichum circinans* (see Table 5.7; Link *et al.*, 1929) and to be present in coloured onion skins but not in white onion skins. White cultivars are susceptible to smudge because they do not produce quercetin (see Fig. 3.3) and therefore cannot form protocatechuic acid. In the presence of water the brown substances in onion skins produce hydrogen peroxide, which is strongly antimicrobial and probably has some protective value (Takahama *et al.*, 2001).

Cell wall material extracted from whole onion bulbs consisted of microfibrils of cellulose and xyloglucan in a crystalline state embedded in a matrix of pectin that was glassy when dry and which swelled to become gel-like when hydrated. The microfibrils behave like solid rods, but they are probably cross-linked by xyloglucan groups (Ha *et al.*, 1997). The tensile strength of the dry skins is much greater than the underlying fleshy scales, and this is thought to result from high levels of calcium cross-linked with pectic carbohydrates (Ng *et al.*, 2000). The dry skins have a much higher ratio of uronic acid-type carbohydrates to neutral sugars (galactose plus arabinose) than fleshy scales. The lack of long galactose side-chains probably increases the degree of calcium cross-linking between uronic acid groups in the pectin molecules, giving greater tensile strength.

WATER VAPOUR ABSORPTION AND TRANSMISSION BY ONION SKIN Onion skins can gain or lose water to their surroundings and tend to equilibrate with the water vapour pressure in their surroundings. Skin water content depends primarily on the relative humidity (RH) of the surrounding air and, to a small extent, on temperature at a given RH. Water contents range from around 4% in equilibrium with air at 16% RH to 38% at 95% RH, and 67% when in contact with water (see Fig. 7.3a; Thamizharasi and Narasimham, 1991; de Matos *et al.*, 1997; Hole *et al.*, 2000). Isolated skins reach hygroscopic equilibrium in about 5 days. The water content of skin in equilibrium with a given RH is higher if water is evaporating from the wet skin than if a dry skin is absorbing water from the air to reach equilibrium, and so the water content of an onion skin in equilibrium with

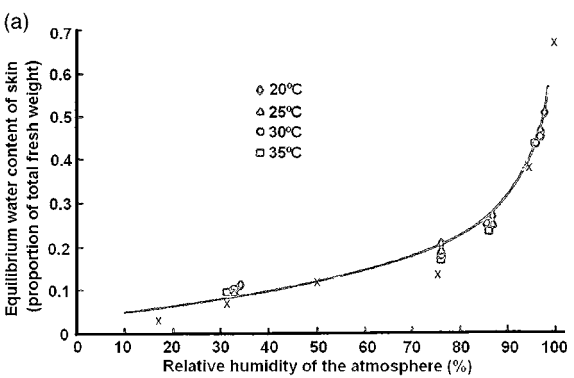
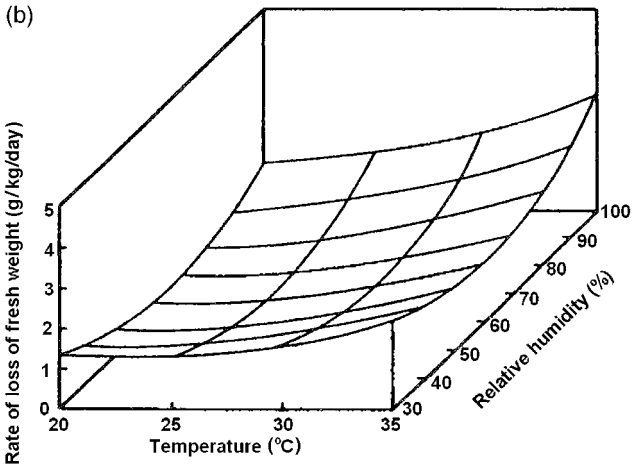
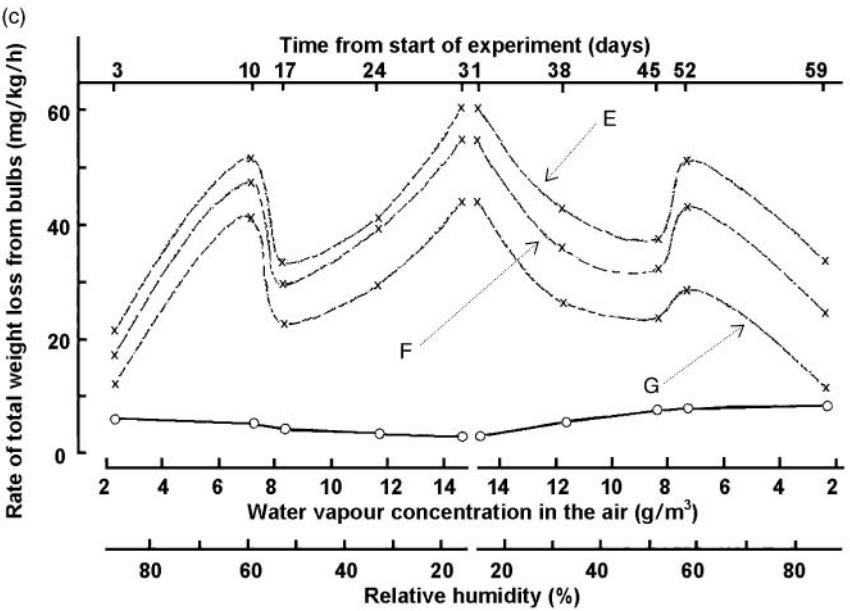


Fig. 7.3. The relationship between the air humidity and onion skin water content, and also the rate of water loss from onion bulbs. (a) The equilibrium water content of the external skins of onion bulbs as determined by the relative humidity of the surrounding air (from de Matos *et al.*, 1997. Courtesy of *Pesquisa Agropecuaria Brasileira*; the data shown as (×) are from the results of Hole *et al.*, 2000). (b) The rate of loss of fresh weight of stored onion bulbs as determined by temperature and relative humidity of the surrounding still air (from de Matos *et al.*, 1997. Courtesy of





Pesquisa Agropecuaria Brasileira). (c) The total weight loss and weight loss due to respiration (the lower, thicker line) under a sequence of vapour pressure deficits, D (or relative humidities, RH) in moving from moist air to dry air between days 0 and 31 and from dry air to moist air between days 31 and 59. The temperature was 20°C and the air was ventilated past the onions. There were three groups of onion bulbs: E, poor skin quality; F, intermediate skin quality; and G, good skin quality (redrawn from Kopec and Eurda, 1989).

the surrounding humidity depends on its previous history of wetting and drying (Thamizharasi and Narasimham, 1991).

Water vapour loss from onion bulbs is largely through the skins rather than the neck or base plate in well-ripened bulbs with tight necks (Thamizharasi and Narasimham, 1988). The driving force for water loss is the difference in water vapour pressure between inside the bulb and the surrounding air. The majority of investigations on water loss from stored bulbs have compared losses at different ambient air RHs rather than vapour pressure deficits (VPDs). Most studies indicate that a store atmosphere of about 65–70% RH is optimal, irrespective of temperature, as this maintains reasonable skin flexibility and avoids the surface dampness that can promote disease or rooting. Rates of water loss at a given RH increase as temperature increases (see Fig. 7.3b), as expected, since VPDs for a given RH increase with temperature. Rates of water loss from stored bulbs do not increase steadily as the RH of the surrounding air decreases, as would be the case if the conductivity of skins to water vapour were constant (see Fig. 7.3b). Onions stored at RHs between 55 and 75% lose water less rapidly than those at higher or lower RH (see Fig. 7.3b).

Another experiment indicates that the conductivity of onion skins to water vapour varies with their water content, since conductivity decreased sharply as the surrounding air decreased from 60 to 50% RH (see Fig. 7.3c). Similarly, as the RH of the surrounding air was subsequently increased, there was a sharp increase in water conductivity of skins between 50 and 60% RH. In this experiment the bulbs were well ventilated, so water loss would be controlled almost entirely by the water conductivity of the skin. Because of this variation in skin conductivity, the rate of water loss from bulbs was not a simple linear function of the VPD gradient between bulb and surrounding atmosphere (Kopec and Eurda, 1989).

One possible clue to the mechanism underlying these changes in conductivity comes from studies on the walls of single epidermal cells from onion fleshy scales stripped of their waxy cuticles (Schonherr and Merida, 1981). Cell wall water conductivity decreased by 50% when RH external to the membrane decreased from 100 to 20%. The effect of RH on membrane water conductivity reflects the balance of polar (water-attracting or hydrophilic) and non-polar (water-repelling) molecular groups in the membrane. In addition, the higher the preponderance of polar groups the greater the tendency of the membrane to swell when wet. A similar explanation at a macroscopic scale may underlie the changes in onion skin water conductivity – and also swelling (see below) – as external RH varies.

At low RH skins are less flexible and tend to split, and this also causes increased water loss (Apeland, 1971). However, the pattern of water-loss response of bulbs differing in skin quality to external RH was essentially the same, although those with inferior skins had more rapid water loss (see Fig. 7.3c).

THE STRENGTH OF ONION SKINS Skin water content strongly affects the flexibility of onion skins (see Fig. 7.4a; Hole *et al.*, 2000). Skins exposed to

95% RH were about twice as resistant to bursting when capping a pressurized tube as skins exposed to 16% RH. Some moist skins could resist burst pressures in excess of 2 MPa, ten times the pressure in a typical car tyre (Hole, 2001). In contrast to this multi-directional breakage test, moist skins failed at the same stress (approx 37 MPa) as a dry skin when stretched in a unidirectional stress and strain test, provided stress (load per unit cross-sectional area) was adjusted for swelling due to water uptake at high humidity. This showed that the breakage stress of a given cross-sectional amount of structural material was the same in dry or moist skin. However, the strain (percentage elongation) of the moist skins averaged 7.9% at breakage and the dry skins 3.5%, and therefore the stiffness (increase in stress per unit strain) of dry skins was more than double that of moist skins (1990 *versus* 850 MPa) (see Fig. 7.4a; Hole *et al.*, 2000), showing the greater flexibility of the moist skin. These visco-elastic properties of the skin may explain why moist skins are stronger in a multi-dimensional burst test but not under one-dimensional directional stretching. If moist skins store energy more readily than dry skins when deformed, they will break at greater loads (Hole *et al.*, 2000).

Comparisons of cultivars and growing conditions – including seasonal, nitrogen fertilizer and irrigation effects, and also time in storage – showed that skin strength increased with the quantity of structural material in the skin cross-section (Hole *et al.*, 2002). This was correlated with, and more accurately and easily measured as, the dry weight of skin per unit area (specific skin weight). Large and consistent differences between cultivars were explained in this way, as was the small increase in skin strength from higher nitrogen applications. The burst pressure of skins was well correlated with specific skin weight (see Fig. 7.4b). The inner skins were more flexible (less stiff) than the outer skins, and the flexibility of inner skins tended to decrease with time, these effects being largely explained by a decrease in moisture content from inner to outer skins and a small decrease in skin water content with time.

Handling damage was simulated by tumbling batches of bulbs inside an internally ribbed drum rotating on a horizontal axis. Proportions of lost and split skins after a fixed 2 min of tumbling at 18 rpm were assessed and related to skin properties. Skin damage decreased with increased skin strength and lower stiffness, but much stronger correlations were found between good quality after tumbling and skin-specific weight, skin thickness and the number of skins. These studies indicated that selection for improved skin quality should be based on selection for increased specific skin weight and skin number, both of which are quite simple to measure (Hole *et al.*, 2002).

During storage, the shape of the bulb slowly changes as inner roots develop from near the growing point and later, as sprout leaves elongate within the bulb (see Fig. 7.5). The elongation near the base of the bulb, associated with inner root growth, causes tensions in the skin in this region that lead to cracks which are mostly vertical, and which then spread towards the top of the bulb,

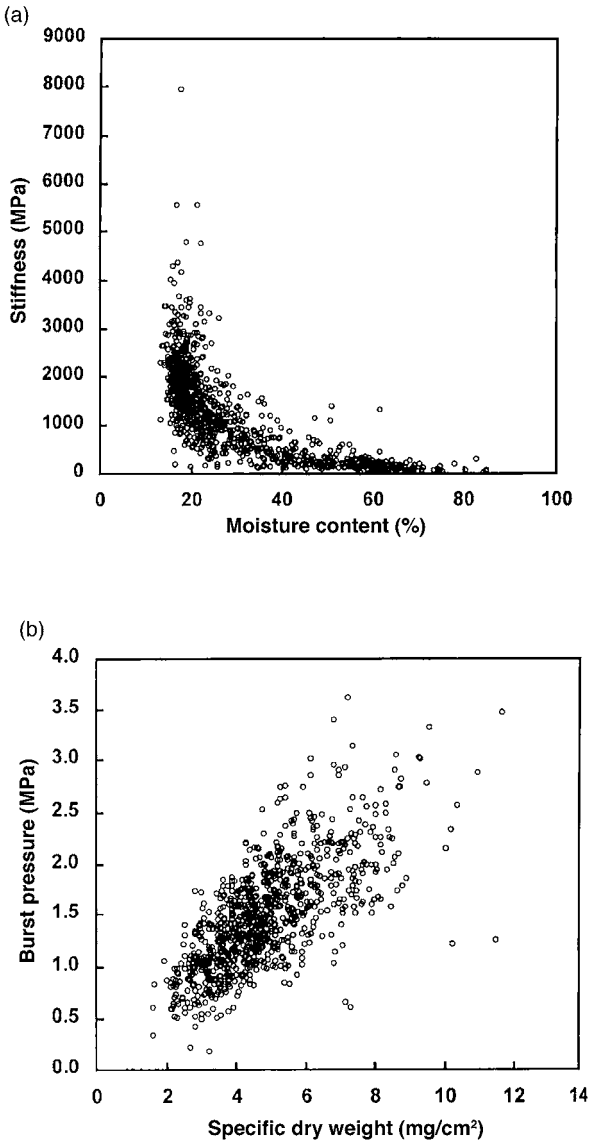


Fig. 7.4. (a) The relationship between onion skin stiffness (the force per unit area of skin cross-section divided by the relative extension in length of the skin under the force) and skin moisture content. (b) The relationship between burst pressure to compressed air of discs of onion skin and the specific dry weight of skin (mg dry weight/cm^2 of surface area) (from Hole *et al.*, 2002. Courtesy of the *Journal of Horticultural Science and Biotechnology*).

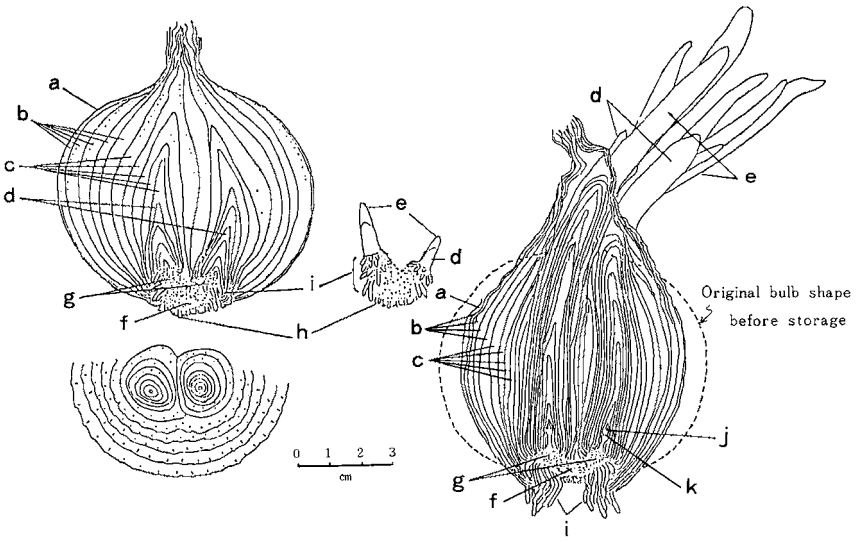


Fig. 7.5. Sections of long-storing, spring-sown onion bulbs 2 months (left) and 12 months (right) after entering storage, showing sprouting, internal root growth and the associated changes in bulb shape: a, skin; b, storage scale from bladed leaf; c, bladeless storage bulb scale; d, sprout leaf with blade; e, sprouting leaves; f, old stem plate; g, new stem plate; h, outer rooting; i, inner rooting; j, spathe; k, developing inflorescence (from Tanaka *et al.*, 1985b. Courtesy of *Research Bulletins, Hokkaido National Agricultural Experiment Station*).

particularly in bulbs that are approaching sprouting (Tanaka *et al.*, 1985c; Tanaka, 1991). All treatments that delay or suppress sprouting, including pre-harvest MH (see below), will help to maintain skin integrity and therefore minimize water loss from the bulbs.

Temperature effects

Abdalla and Mann (1963) stored bulbs of two cultivars – 'Excel', with a short storage life and 'Australian Brown', with a long storage life – at constant temperatures of 0, 5, 10, 15, 20, 30 and 40°C. After 0, 2, 4, 8 and 16 weeks of storage, samples of 30 bulbs were planted on moist peat at 15°C, and the time for 50% of the bulbs to sprout visibly was recorded. For both cultivars the rate of sprouting was fastest in bulbs stored at 10–15°C and was slower at both lower and higher temperatures (see Fig. 7.6).

The rate of elongation of sprouts within the bulb, and the rate of leaf initiation, were much faster at 15 than at 0 or 30°C (see Fig. 7.7). Therefore, the rate of sprout development in onion bulbs, unlike most physiological processes, does not increase in rate progressively as temperature increases. More recently,

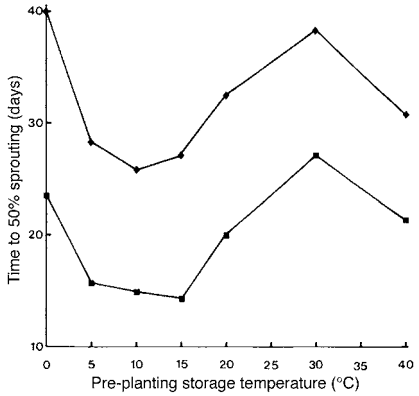


Fig. 7.6. The time to 50% sprouting after planting on moist peat at 15°C of two onion cultivars previously stored for 4 weeks at the temperatures shown: the long-storing cv. 'Australian Brown' (upper) and the short-storing cv. 'Excel' (lower) (data from Abdalla and Mann, 1963).

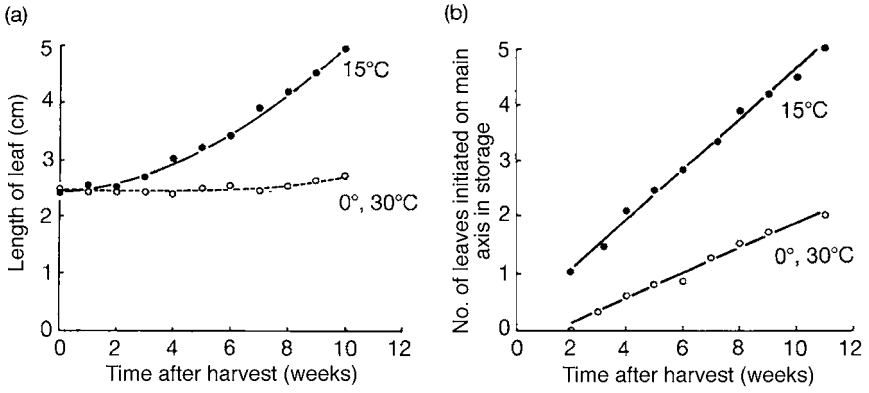


Fig. 7.7. (a) The effect of storage temperature on the sprout elongation of cv. 'Excel'. (b) Leaf initiation in cv. 'Excel' stored at constant temperatures (from Abdalla and Mann, 1963. Courtesy of *Hilgardia*).

in a study of ten cultivars including Japanese, Dutch and North American globe types, rate of sprouting in storage was found to be slower at 5 and at 30°C than at intermediate temperatures in all cultivars. Optimum temperatures for sprouting ranged from 10 to 20°C, depending on cultivar (Miedema, 1994a). A similar temperature response of sprouting was observed in cv. 'Texas Grano 1015Y', and respiration rate mirrored the response for the first 8 weeks of storage, but at 12 weeks it increased progressively with temperature (see Fig. 7.8; Yoo *et al.*, 1997).

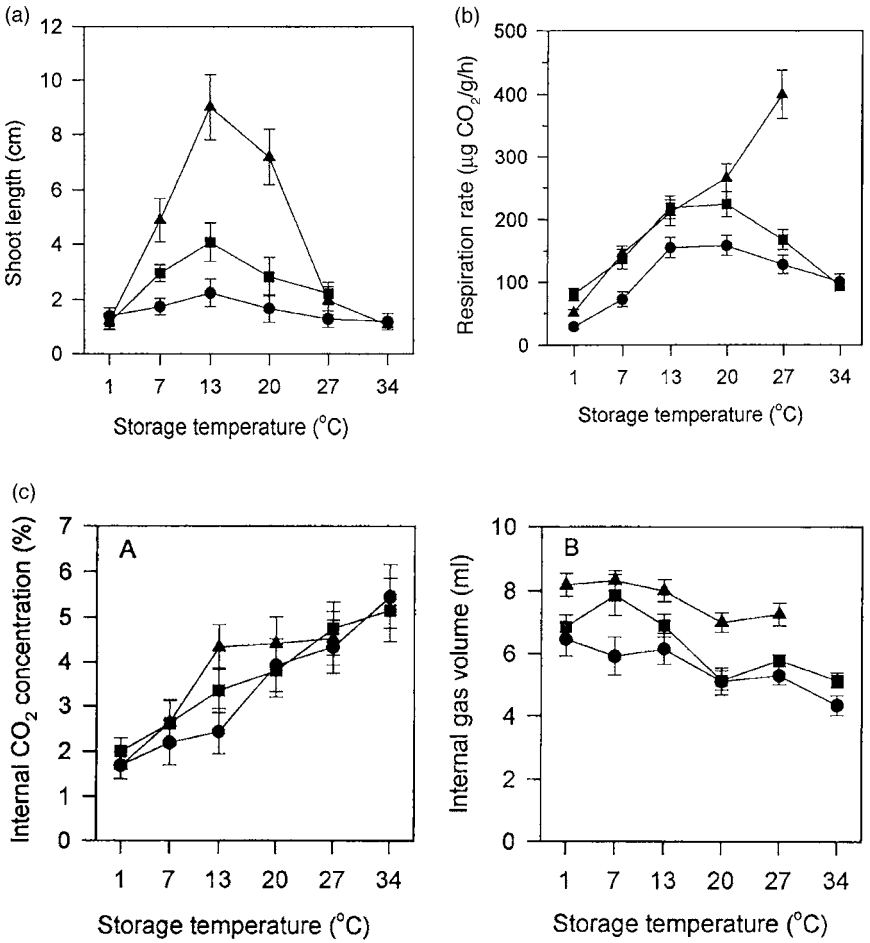


Fig. 7.8. Sprouting, respiration rate and internal CO_2 concentrations in bulbs of onion cv. 'Texas Grano 1015Y' stored at different temperatures after 4 (●), 8 (■) or 12 (▲) weeks. The error bars show standard deviations based on ten replicates. (a) Internal shoot lengths. (b) The respiration rate of the centre scales. (c) Internal CO_2 concentration (A) and internal gas volume (B) (from Yoo *et al.*, 1997. Courtesy of *Postharvest Biology and Technology*).

The rate of sprouting is more rapid in bulbs transferred from 0 or 5 to 25°C than in those kept continuously at 25°C (Tanaka *et al.*, 1985a). Bulbs stored at 25°C for 5 months and then transferred to 2°C subsequently had a lower respiration rate than those stored at a constant 2°C (Ward, 1976). The reasons for these effects are not known, but they do indicate that some long-lasting dormancy-enhancing process is engendered by storage at 25–30°C. Storage at these temperatures also inhibits cytokinin activity (see below), has a devernalizing

effect following flower induction (see Fig. 4.39) and delays bulbing in plants grown from stored bulbs (see Figs 4.33 and 4.39). It would be interesting to know whether there is any underlying connection for these various remarkable effects of temperatures around 25–30°C on the physiology of onion bulbs.

Once sprouting has occurred in rooted bulbs, sprout growth rate increases progressively with temperatures in the range 0–25°C, typical for a growth response in onion (see Fig. 4.22). Therefore, during rooting and sprouting there must occur a transition from the remarkable growth-inhibitory effect of temperatures around 30°C to the usual increase of growth rate with temperatures in the range 10–30°C. As dormancy declines during bulb storage, probably at different rates in different individual bulbs, the transition between these two contrasting temperature responses may give confusing transitional temperature responses.

High temperatures applied to bulbs immediately after harvest can increase their subsequent rate of sprouting. Compared with cooler temperatures, 30 or 35°C for 3 weeks after harvest accelerated sprouting in subsequent dry storage at 15°C, and also rooting and sprouting in bulbs planted on moist vermiculite at 15°C. In bulbs that were not mature at harvest, a postharvest temperature as low as 25°C had such an effect (Miedema, 1994a). Such high temperatures are often used to cure freshly harvested bulbs, and this evidence indicates that this practice may shorten storage life. A similar effect of high temperatures around harvest time occurs in garlic (see 'Garlic Dormancy and Storage', below).

In summary, onion bulbs pass through three phases in relation to the effects of warm temperature on sprouting (Miedema, 1994a). Immediately after harvest, periods of a few weeks at 25–35°C reduce dormancy and result in earlier sprouting. Subsequently, long-term storage at 25–30°C retards sprouting. Then, once bulbs are rooted and growing, such temperatures are optimal for sprout growth, typical of a vegetative growth process in onion.

Cultivar effects

In a comparison of ten cultivars planted on moist vermiculite at 10°C, time to 50% sprouting ranged from 49 to 156 days, depending on cultivar, and time to 50% sprouting in dry storage at 10°C ranged from 149 to 310 days. There was a large bulb-to-bulb variation in time to sprouting within long-storing cultivars (see Fig. 7.9).

Differences between cultivars also occur within the range of 0–56 days in the time when sprout leaves begin to elongate at the shoot apex (Bufler, 2001; in press, a; Yasin and Bufler, 2007). From observations on bulbs dry-stored at 18°C, cultivars divided into two classes, with several intermediate types (Bufler, in press, a). Type 1 cvs, which were all of the type 'American Globe', had a period of up to 8 weeks after curing with no sprout leaf growth, and could therefore be defined as truly dormant. Type 2, which were all 'Rijnsburger' (Dutch) cvs, started sprout leaf growth immediately after curing, and hence showed no period of true dormancy. Interestingly, the 'Rijnsburger' types include some of the longest-

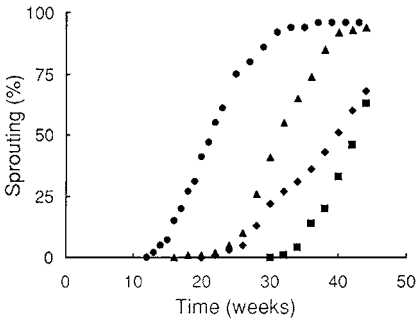


Fig. 7.9. The time course of sprouting in dry storage at 10°C of onion cvs 'Radar' (●), 'Hyton' (▲), 'Rocardo' (♦) and 'Copra' (■) (from Miedema, 1994a. Courtesy of the *Journal of Horticultural Science and Biotechnology*).

storing cultivars, indicating that their long storing capability results from slow elongation of sprout leaves within the bulb rather than a long period of true dormancy with no sprout leaf elongation.

The ranking of cultivars in this respect remains similar when they are grown in a wide range of soils and climates and stored in a variety of conditions (Magruder *et al.*, 1941). Duration of dormancy – and therefore storage potential – clearly depends on genotype (see Chapter 1, 'Onion Cultivars') and can be improved by breeding. Long storage potential is correlated with high bulb dry matter content, high pungency and the formation of several thick skins (Currah and Proctor, 1990).

Effects of roots

As a comparison of sprouting times in Figs 7.6 and 7.9 indicates, bulbs sprout much more rapidly if they are planted on moist substrate and allowed to root than if they are kept in dry storage, which inhibits rooting. Tanaka *et al.* (1985b) distinguished two types of rooting. First, there is 'outer rooting', which is the formation of roots on the old stem plate of the bulb; and, secondly, 'inner rooting', which is the formation of new roots deeper within the bulb, near the shoot apex at the base of the developing sprout. Inner rooting usually accompanies internal sprout growth, although its extent appears to vary with cultivar. Outer rooting is promoted by wetness at the base of the bulb and can occur in store if humidity is high, e.g. above about 80% RH. Inner rooting is not affected by the humidity external to the bulb until the roots penetrate the surface of the bulb. Thereafter, the growth rate of inner roots is increased by high humidity and wetness.

When bulbs are stored at different temperatures and then planted on moist substrate at 10–15°C, roots can be visible within a few days, much sooner than visible sprouts. In the comparison of ten temperate cultivars planted on moist

vermiculite at 10°C, mentioned in the previous section, time to 50% rooting varied from 8 to 63 days depending on cultivar, and there were large bulb-to-bulb differences within a cultivar in time to root appearance (Miedema, 1994a). For all cultivars, rooting was most rapid at 10°C and was very slow at 30°C. Therefore, temperature responses of rooting were similar to, but faster than, those of sprouting.

If root initials are regularly removed from bulbs planted on moist substrate, sprouting is inhibited. For some cultivars this inhibition can be reversed by including the cytokinin benzyl adenine (BA) in the solution (see Table 7.1). In addition, wounding the base plate accelerates sprouting and increases the effectiveness of BA in promoting sprouting of de-rooted bulbs (Miedema, 1994c). Roots are initiated from the periphery of the primary thickening meristem (PTM) in bulbs (see Fig. 2.10). An absence of starch granules in the PTM is associated with root dormancy. When bulbs are stored at high temperatures (30°C), starch remains undetectable in the PTM and roots do not initiate. However, if BA is injected into such bulbs the shoots begin sprout growth, although starch remains undetectable in the PTM (Ernst *et al.*, 1999). These experiments indicate that the acceleration of bulb sprouting that is associated with the growth of roots may be caused by cytokinins produced in the roots.

Bulb respiration rates and carbohydrate metabolism

Dormant onion and garlic bulbs have remarkably low rates of respiration when compared with other vegetable crops (see Table 7.2). In storage, as time progresses, the rate of respiration increases (see Fig. 7.10). Respiration rates increase with temperature (see Figs 7.8b and 7.10) but, for intact dormant bulbs, the rate of increase with temperature is remarkably low. At a temperature of 40°C

Table 7.1. The effects of root presence (+) or removal (–) and 10 μmol/l benzyl adenine (BA) on the sprouting in water culture of bulbs of four onion cultivars and of shallot cv. 'Noordhollandse Strogele'. Values are expressed as the percentage of bulbs with visible sprouts. Within columns, data followed by the same letter are not significantly different at $P < 0.05$ (from Miedema, 1994c).

Treatment						
Roots	Medium	'Radar'	'Stentor'	'Copra'	'Hyton'	Shallot
Intact	Water	50^{b}	50^{a}	50^{a}	50^{a}	50^{a}
Removed	Water	7^{d}	2^{c}	0^{c}	0^{b}	0^{b}
Removed	BA	60^{a}	31^{b}	16^{b}	12^{b}	7^{b}
Time to 50% sprouting with roots in water (days)		11	13	15	31	16

Table 7.2. Respiration rates (CO_2 output, mg/kg/h) at constant temperatures in air of onion bulbs, leeks, garlic and a selection of root, shoot and leafy vegetables (from Robinson *et al.*, 1975, Table 1; data for garlic from Kader, 1992).

	Temperature (°C)				
Vegetable	0	5	10	15	20
Onion bulbs, 'Bedfordshire Champion'	3	5	7	7	8
Garlic bulbs	–	5–10	–	–	–
Leeks, 'Musselburgh'	20	28	50	75	110
Potato, 'King Edward'	6	3	4	5	6
Cabbage, 'Decema' (storage type)	3	7	8	13	20
Carrots	13	17	19	24	33
Lettuce, 'Kloek'	16	24	31	50	80
Spinach	50	70	80	120	150

respiration rates increase quite sharply, possibly because these temperatures are injurious to bulbs.

The Q_{10} for respiration rate in fully dormant bulbs over the temperature range 10–30°C is about 1.3. If bulbs are wounded, their rate of respiration increases and reaches a maximum after about 12 h. In this condition the Q_{10} for bulb respiration rate is about 2.3, more normal for a physiological process (Miedema, 1989). As dormancy declines and internal sprout growth begins, bulb respiration rates increase more rapidly with increases in temperature, and Q_{10} values are similar to most plant tissues. The respiration rate of damaged bulbs remains elevated for many weeks after the initial damage, though in less severe cases it can eventually return close to the level of undamaged bulbs.

Irradiation with 150 or 300 Gy of gamma radiation increased respiration rates by 35 and 100%, respectively, 24 h after treatment in onion bulbs cv. 'Rouge d'Amposta' stored at 20°C. Within 2 weeks of treatment the respiration rate of irradiated bulbs was down to the level of untreated controls (Benkeblia *et al.*, 2000). Ionizing radiation probably causes cellular damage and stimulates repair metabolism as does mechanical damage, and hence increases respiration rates. In the longer term the respiration rate of irradiated bulbs continued to decline slowly, while that of untreated bulbs began to increase (see Fig. 7.10). The Q_{10} of respiration rate in untreated bulbs increased from 1.8 to 2.9 during 2 months of storage at 4°C but the Q_{10} of irradiated bulbs did not increase over this interval.

The relationship between respiration rates of stored produce in reduced-oxygen atmospheres has frequently been described by the Michaelis-Menten equation, where respiration rate is plotted against oxygen concentration. According to this model, bulb onions had a K_m value (oxygen concentration at which respiration rate was half of maximal) of 1.6 kPa (equivalent to 1.58% oxygen partial pressure in a standard atmosphere) at 4°C (Benkeblia *et al.*, 2000), similar to the value reported for green *Allium fistulosum* (see 'Green Onion Storage',

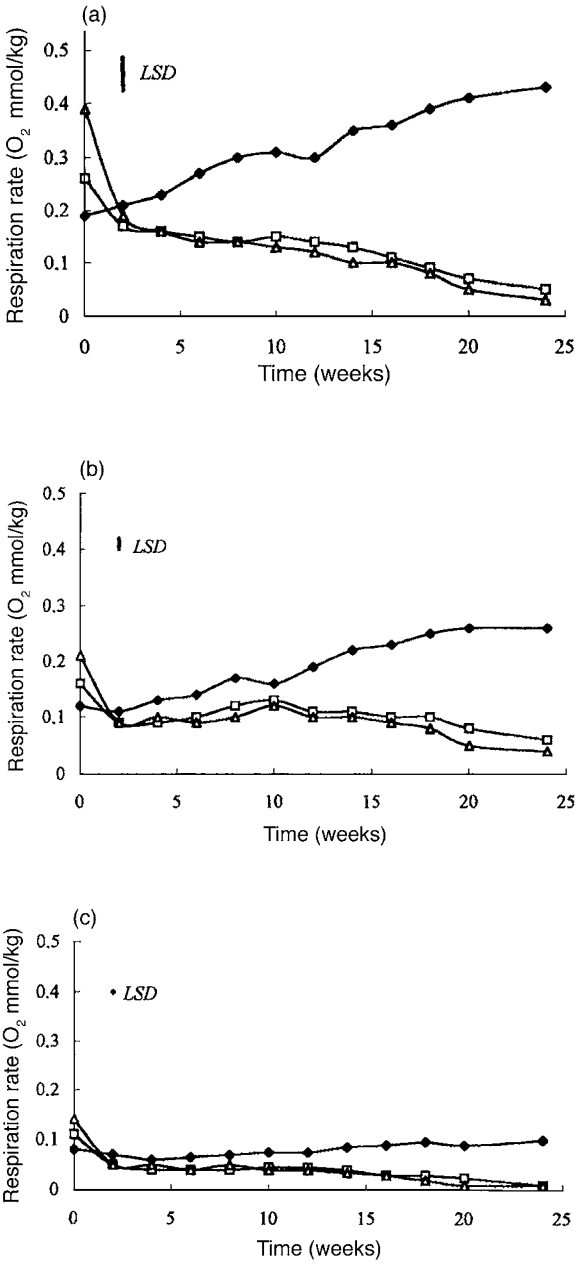


Fig. 7.10. Variation in the respiration rate of onion bulbs of cv. 'Rouge Amposta' after gamma irradiation with 0.15 kGy (□), 0.30 kGy (△) or without irradiation (◆), followed by storage at 20°C (a), 10°C (b) and 4°C (c) (from Benkeblia *et al.*, 2000. Courtesy of the *Journal of the Science of Food and Agriculture*).

below). However, at 20°C, unlike green onion, K_m was higher, and this equation did not fit the data very well; it yielded an approximate 'apparent' K_m of 6.3 kPa (equivalent to 6.2% oxygen in the atmosphere).

It is likely that the long diffusion path of oxygen into bulbs (see below) is partially rate limiting for respiration. This makes the Michaelis-Menten equation inappropriate for describing respiration rate kinetics in a bulky organ like the onion bulb, whereas it is appropriate for the leafy tissue of green salad onions, which has a much shorter diffusion path from the free atmosphere to respiring cells.

If the dry, outer skins of onions are removed, the respiration rate of bulbs increases nearly twofold and the rate of water loss also increases (Apeland, 1971). Bulbs with the skin removed also sprout more rapidly than those with intact skins (Tanaka *et al.*, 1985a). Intact dry, outer skins may act as a strong barrier to gas diffusion, resulting in the decreased O_2:CO_2 ratio found within stored bulbs (see Fig. 7.8). Increased CO_2 and decreased O_2 prolongs the time to bulb sprouting, compared with storage in air (see 'Controlled atmosphere storage', below). It has been suggested that intact outer bulb skins maintain an internal atmosphere within the bulb, which slows both respiration rates and sprouting growth (Ladeinde and Hicks, 1988). Furthermore, wounding, which promotes sprouting, may, by puncturing the skin, change the internal atmosphere of the bulb, particularly since sealing cuts with wax nullifies this effect on sprouting (Boswell, 1924). However, Yoo *et al.* (1997) found that sprout growth was not inhibited by internal carbon dioxide concentrations raised to 7.9% by sealing bulb necks.

Starting at the end of bulbing and before harvest, fructan (see Chapter 8) concentrations decline and fructose levels increase in storage scales, most rapidly in the outermost scales. Fructan concentrations increase in the bulb base plate, and it appears that this acts as an intermediate store for carbohydrates to supply the developing sprout. The decrease in fructan and increase in fructose with time is not prevented by storing bulbs in ethylene concentrations that inhibit sprout leaf growth (Bufler, in press, b). Dry weights of storage scales decline and base plate and sprout weights increase during storage, reflecting this translocation of carbohydrates. The sprout always contains enough carbohydrate for growth (50–60 mg/g dry weight, of which 30% is fructan), and therefore growth is not limited by the source of supply of carbohydrates. As sprouts grow, sucrose synthase enzyme activity increases, indicating an increasing sink strength for carbohydrates (Pak, *et al.*, 1995; Yasin and Bufler, 2007).

From a large number of individual bulb measurements on two cultivars with a clear dormant period, as shown by the absence of sprout leaf elongation (see 'Cultivar Effects', above), it was found that ATP content and sucrose synthase enzyme activity increased within both the sprout leaves and enclosed apical tissues when initial sprout leaf growth occurred (Yasin and Bufler, 2007). These increases were concomitant with a small increase in total bulb respiration rate. Increases in water-soluble carbohydrates and fructans were detectable in the

stem plate and sprout leaves, commencing before sprouting and continuing to increase as sprouting occurred. These fractions decreased in the inner scale leaves, suggesting the mobilization of storage carbohydrates from their 'source' in the scale leaves via the stem plate to a 'sink' in the sprout leaves, where they were utilized in the biosynthesis and respiration of sprout leaf growth (Yasin and Bufler, 2007).

Effects of harvesting time

Several studies have shown that, in order to maximize the time to sprouting in store, it is best to harvest before the bulbs have reached their maximum weight, probably when 50–80% of plants have reached the stage of 'soft-necks' and foliar collapse (Komochi, 1990). Harvesting later frequently results in poor skin quality and, as described above, the loss or puncturing of skins in stored bulbs accelerates sprouting.

The role of growth regulators

Growth-inhibitory substances have been extracted from dormant bulbs by a number of workers (Komochi, 1990). Stow (1976) found growth inhibitors in the leaves of onions during bulbing, and postulated that these were translocated to the bulb and were responsible for maintaining its subsequent dormancy. He found that early defoliation or leaf desiccation of bulbs resulted in earlier sprouting, and suggested that this was because the inhibitory substance had not been fully translocated from leaf to bulb before defoliation (see Fig. 7.11).

Abscisic acid (ABA) was detected within bulbs, but the amount corresponded to only 10–20% of the growth-inhibitory activity found in bulb extracts. Increases in ABA concentration and its subsequent decline correlate well with the onset and decline in dormancy in bulbs of *A. wakegi* (see Fig. 4.46). Chope (2006) found that ABA concentrations in onion bulbs declined exponentially during storage and that sprouting occurred at the minimal ABA concentration, but bulb soaks or pre-harvest sprays with ABA or an ABA analogue (8′-methylene ABA methyl ester) failed to increase internal ABA concentrations and prolong dormancy.

Exposure of bulbs for 24 h to an atmosphere containing 1 μl/l of 1-methylcyclopropene (1-MCP) retarded sprouting in bulbs stored at 4 or 12°C but not at 20°C storage (Chope *et al.*, 2007). Carbohydrate metabolism was inhibited in bulbs stored at 12°C. 1-MCP is an inhibitor of ethylene perception by plant tissue, suggesting an involvement of ethylene in onion bulb dormancy. Continuous exposure to 10 μl/l of exogenous ethylene gas inhibits the elongation of sprout leaves in stored bulbs (Bufler, in press, b) and is rapidly being adopted to prevent sprouting in commercial stores (see 'Controlled Atmosphere Storage', below).

Levels of growth hormones are low in dormant bulbs but, as sprouts start to develop, increases in cytokinin – followed by gibberellin, then auxin – activity

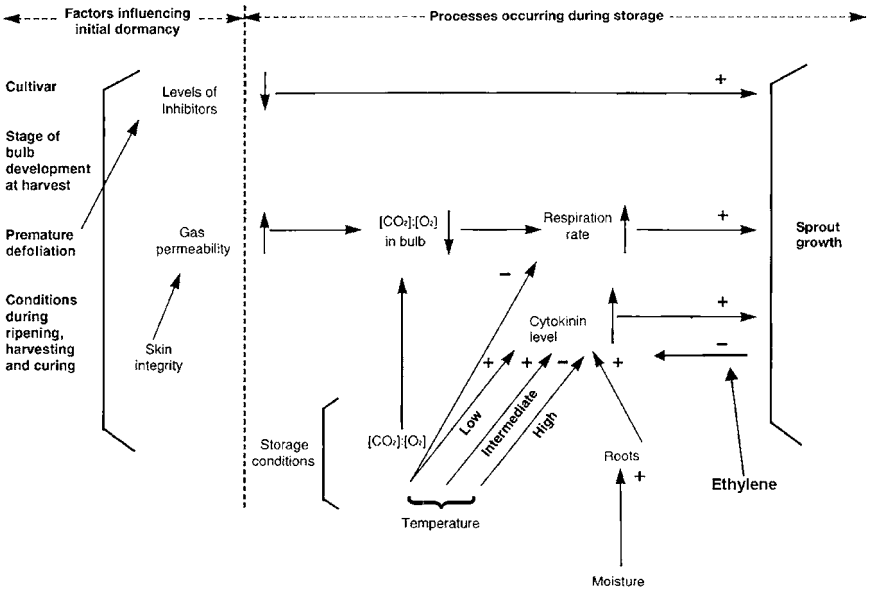


Fig. 7.11. Summary of the main factors influencing the rate of sprouting in stored onion bulbs. ↑ indicates an increase, ↓ a decrease in the level of a factor; + a promoting effect and – a retarding effect of the conditions indicated on a process or the level of a factor.

have been reported. Storage of bulbs at warm temperatures (25–30°C) prevents the rise in cytokinin activity that occurs in bulbs stored at cooler temperatures. Furthermore, sprouting can be stimulated in warm-stored bulbs by injecting them with cytokinins (Miedema, 1994b). These results indicate that inhibition of sprouting by high-temperature storage is due to a low level of endogenous cytokinins. As described previously, the promoting effect of roots on sprouting seems to be due to cytokinin production by the roots.

Summary

The internal control of sprouting remains uncertain. It has been debated whether the onion bulb is ever truly dormant except immediately around harvest time (leaf collapse), when sprout leaf elongation ceases in some cvs (Bufler, 2001) and mitosis ceases (see Fig. 7.2), since mitosis resumes a few weeks after harvest. Carbohydrate metabolism does not appear to be the factor limiting sprout growth inside bulbs since levels of sucrose, sucrose synthase and fructans at the shoot apex are high throughout storage, but sprouts do not show the growth that this could support (Pak *et al.*, 1995).

It has long been known that wounding bulbs accelerates sprouting (Boswell, 1924). One reason for this may be the release of growth-promoting substances upon wounding, the so-called wound hormones. However, change

in the internal atmosphere as a result of damage to the bulb skin is another possible cause of sprouting. Growth-inhibitory substances appear to be involved in the induction and maintenance of dormancy, and ABA is implicated, but there may be other inhibitors involved. Evidence indicates that cytokinins produced by root initials act at an early stage in the breaking of dormancy. Dormancy and sprouting may be controlled by the balance between growth-promoting and growth-inhibitory substances within bulbs (Komochi, 1990). Figure 7.11 summarizes the main factors influencing bulb dormancy.

The technology of bulb onion handling and storage

Techniques of harvesting, curing and storing onion bulbs have been developed that utilize artificial drying and air conditioning, and make it possible to store bulbs in bulk to a depth of about 3 m for up to 9 months after harvest (MAFF/ADAS, 1982; see Plate 10). Both traditional and fully mechanized techniques of harvesting are described in Chapter 6.

The mechanical handling of onion bulbs at harvest, storage and packing

The harvesting of onion bulbs and their transfer to storage and, after storage, their grading, packing and dispatch to market inevitably involves some impacts that can damage quality. Skin loss and splitting is one quality consideration, while the strength of skins depends on the amount of structural material in skin cross-section, largely a varietal feature; the flexibility of skins depends on their moisture content (see 'The Strength of Onion Skins', above). Conditions within a bulk store can never be exactly uniform; for example, temperature and humidity changes used in store control are more abrupt close to ventilation ducts, and this results in more skin damage in these regions of the store (Brice, 1994). In preparing stored onion bulbs for market it can be desirable to lose a dirty outer skin, but it is important to retain inner skins unsplit. Relative humidity of 75% during post-storage warming and handling is optimal for skin retention (Brice, 1994).

Onion quality can be impaired by internal bruising that is not easily recognizable. Bruising causes the tightly packed concentric rings of the onion to slide past each other and break the seal between them, leading to internal spaces where tissue juices accumulate; these may become a substrate for rot-causing microbes (Maw *et al.*, 1995). These internal voids can be detected as 'edges' in X-rays of bulbs, and this provides a possibility for non-destructively detecting internally damaged bulbs (Shahin *et al.*, 2002). Bruised areas also show up as yellow-stained when bulbs are placed in concentrated hydrochloric acid (Maw *et al.*, 1995).

Internal bruising was detectable with a fall of just 10 mm on to a steel surface using bulbs of a hard, storage-type cultivar (Timm *et al.*, 1991). Instrumented spheres acting as 'artificial onions' have been used to investigate the

number and intensity of impacts bulbs are subject to during harvesting and storing (Herold *et al.*, 1998) and grading and packing and for market (Timm *et al.*, 1991). These spheres record the number of impacts above a pre-set threshold level, and the peak load and load integral of each impact to which they are subject. Experiments show that dropping on to a hard steel surface gave greater peak forces than drops on to stretched conveyer belts. Various measures of impact force in drops from different heights on to these surfaces have been related to measures of damage suffered by onion bulbs given these dropping treatments.

Damage manifests as increased respiration and water loss and an increased number of bulbs rotting, all contributing to loss in marketable weight at the end of storage. The respiration rate of bulbs subject to minor impacts declines with time to the level of non-dropped bulbs, but that of bulbs dropped six times from a height of 1.05 m on to steel remained about double that of controls throughout a 10-week storage period (see Fig. 7.12).

An increased accumulated respiration over a 19-day period was the most sensitive indicator of dropping damage in these experiments. If only a few impacts occur, the peak force experienced is more damaging than the total load integral, but with numerous impacts the load integral is a better predictor than peak force of damage. From these results and data from multiple passage of an instrumented sphere through harvesting machinery, the extent of losses likely to be caused by

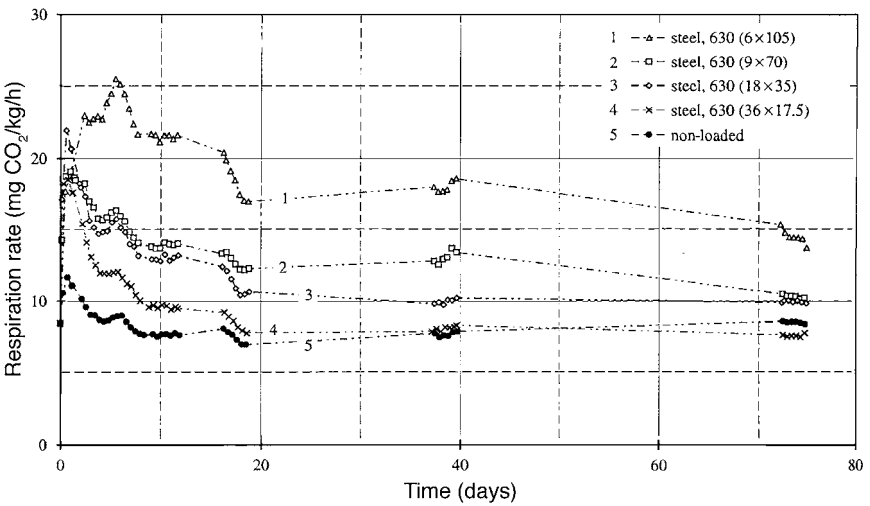


Fig. 7.12. The effects on respiration rate of dropping onion bulbs (cv. 'Rijnsburger Balstora') on to a hard steel surface. The sum of the dropped heights was always 630 cm, but was made up of a few high drops or many short drops, as detailed (in cm) in the top right-hand corner of the graph. Larger and more prolonged increases indicate greater and more permanent internal damage (from Herold *et al.*, 1998. Courtesy of the *Journal of Agricultural Engineering Research*).

impact damage can be estimated. Using this analysis in handling machinery and systems, features causing unacceptably high impact forces or frequencies can be identified and improved. In bulk stores, onions at the bottom, which may be 5 m deep, are subjected to a greater static load than those at the top and this can also lead to damage, as indicated by a greater respiration rate (Herold *et al.*, 1998).

Bulb treatments to prevent sprouting in storage

Apart from decay due to disease, internal sprout growth is the primary cause of the changes that lead to the deterioration of stored bulbs. Therefore, if sprout growth can be delayed or prevented, bulb storage life can be extended. Pre-harvest applications of sprout-inhibiting chemicals and postharvest exposure of bulbs to ionizing radiation have both been developed to prevent sprout development in stored onion bulbs.

PRE-HARVEST APPLICATION OF MALEIC HYDRAZIDE, A SPROUTING INHIBITOR Maleic hydrazide (MH) is a growth-regulatory substance that disrupts cell division (Isenberg *et al.*, 1974). If applied to onion leaves while they are green and actively exporting photosynthates, MH is translocated to the shoot apex, where it prevents cell division. In stored bulbs this suppresses sprout and root growth. The increase in cytokinin and other growth-promoting substances, and decrease in growth inhibitors associated with sprout development, does not occur. In untreated bulbs respiration rates increase rapidly as they approach sprouting, whereas this increase is much lower in MH-treated bulbs (Ward and Tucker, 1976).

A minimum concentration of 20 ppm MH at the centre of bulbs is required reliably to suppress sprout growth. To achieve this, the timing of applications in relation to the stage of crop development is important. The MH needs to accumulate at the growing point when bulbs are nearly mature, and have therefore completed the cell division required to form bulb scales and sprout leaf initials, but it must be applied while the leaves are still green and actively translocating. Application too early results in the development of bulbs with abnormal, soft, 'spongy' centres. Application rates in the range 1.1–5.7 kg/ha in aqueous solution have been tested, and the lower to middle part of this range has proved effective (Komochi, 1990).

Because the amounts absorbed and translocated from foliar sprays will vary with weather conditions and the state and activity of the leaves, the optimum quantity to apply is subject to some uncertainty. In the UK it is recommended to apply 8.4 l/ha of 36% active ingredient (a.i.) MH when the crop has reached the stage of 10% fall-down and, in The Netherlands, application at a similar rate and stage is recommended. Studies from the USA and Poland indicate that applications at 50% fall-down are best. The difference between these two sets of recommendations may be because bulbs are harvested at a later developmental stage in the USA and Poland. A period following spray application of at least 10 h without rainfall is needed for MH absorption.

Because of the importance of the stage of bulb development at which MH is applied, the best results occur when all plants in the crop are at the same stage of development. Such a crop requires plants of a uniform cultivar, a small spread in emergence date, and an even plant density and uniform growth that have not been checked differentially by limitations of nutrients and water or by pest, disease or herbicide damage.

IRRADIATION A disruption of cell division at the shoot apex and inhibition of sprout growth similar to that caused by MH can be achieved by treating dormant bulbs with γ (gamma) irradiation (Komochi, 1990; Gubb and MacTavish, 2002). Doses of 20–150 Gy are sufficient to prevent sprout growth, and Benkeblia *et al.* (2000) showed that doses of 150 Gy (0.15 kGy) cause only a small initial increase in respiration rate (see Fig. 7.10). Doses in this range cause no detectable differences in the taste or nutritional composition of the bulbs. Much higher doses can reduce the content of flavour-determining compounds.

To be effective, the bulbs must be irradiated soon after harvest while fully dormant. Delay in irradiation decreases effectiveness as sprouts develop internally. How long it can be delayed depends on both the duration of dormancy of the cultivar and the temperature of storage. The long-storing cv. 'Senshuki' was strongly inhibited from sprouting when treated 2–3 months after harvest, but the short-dormancy cv. 'Sapporoki' had to be irradiated within 1 month of harvest (Komochi, 1990). If internal sprout development is slowed by storage at low temperatures (0–5°C), then the time available for effective irradiation is increased.

A darkening of tissue near the growing point has frequently been observed to develop a few weeks after irradiation. This can be prevented by low-temperature (0–5°C) storage of treated bulbs, but darkening develops several weeks after bulbs are returned to normal ambient temperatures. Ultimately, cell death and decay occur in irradiated bulbs, after 25–30 weeks in the case of cv. 'Rouge d'Amposta' (Benkeblia *et al.*, 2000).

No harmful effects have been observed in numerous toxicological tests using irradiated onions. Because there are no toxic effects or serious detrimental effects on eating quality, the sale of irradiated onions is permitted in many countries, and in many of these the irradiation of shallot and garlic bulbs for sprouting inhibition is also permitted (Komochi, 1990).

Onion storage systems

Some of the physiological information discussed above has been applied in the development of appropriate techniques of onion storage. In particular, since temperature, humidity and gas atmosphere requirements for long-term storage are known, air conditioning and ventilation techniques have been developed that allow these needs to be met in large-scale, bulk stores. The onion bulb is a natural food store for the plant, but it is a living system undergoing a process of development towards sprouting, and subject to decay by various disease-

causing organisms. The object of storage technology is to maintain the bulb for as long as possible in an unchanged, sound condition and, as far as possible, to provide a bulb that has a shelf-life, after removal from store, of several weeks, to allow for transport and marketing before deterioration.

Knowledge of the physiology of dormancy and the epidemiology of storage disease (see Chapter 5) indicate the requirements for long-term storage. Systems to provide these conditions in store can be engineered using the physical principles of temperature and humidity control, and taking account of economic and technological constraints. Two basic strategies have been applied. The first is to maintain the store temperature as low as possible, but above that causing freezing damage (–2°C); the second is to exploit the high temperature dormancy of onion bulbs and to try to maintain stores close to 30°C. The first strategy is widely used in temperate regions like north-western Europe, while the second is more appropriate for the storage of bulbs in tropical conditions, where refrigeration is expensive and electrical power unreliable (Currah and Proctor, 1990).

In addition to cold storage, controlled atmospheres with lowered oxygen concentrations and increased carbon dioxide levels are widely used, particularly for high-value bulb crops, for example the sweet 'Vidalias' of Georgia, USA. The use of ethylene gas to prevent sprouting in storage may become an important new technique (see 'Controlled Atmosphere Storage', below).

The physiological and pathological processes that proceed within a store of onion bulbs interact with the physical processes of heat and water vapour exchange so as to mutually influence the environment within the store. Figure 7.13 summarizes the main factors that influence storage and indicate how they interact. With time, sprouting and internal root development proceed within the bulbs; these change bulb shape, tension the skins, and crack skins. This will increase the conductivity of skins to water vapour and therefore the rate of water loss from the bulbs. As sprouting proceeds respiration will increase (see Fig. 7.10), causing increased outputs of heat, carbon dioxide and water vapour by bulbs. The rate of heat production due to metabolic processes in kcal/t/h is approximately equal to the CO_2 output rate, in mg/kg/h, multiplied by 2.6 (Burton, 1982).

Bulb deterioration due to disease will also increase respiratory outputs. Because of increasing water loss and respiration, the ventilation needed to maintain RH at 65–70% and the cooling or ventilation needed to dissipate heat produced by the bulbs will tend to increase with time.

Probably more significant, in practice, are the differences in conditions within the store caused by variations in outside temperatures and air humidities. Outside temperatures and solar radiation will obviously influence the rate of loss or gain of heat by conduction and radiation, and this will be influenced by the design and insulation of the store. The temperature and relative humidity of air drawn into the store will also determine its capacity to cool or heat, and to moisten the air and the onions in store. If warm air is drawn into an onion store

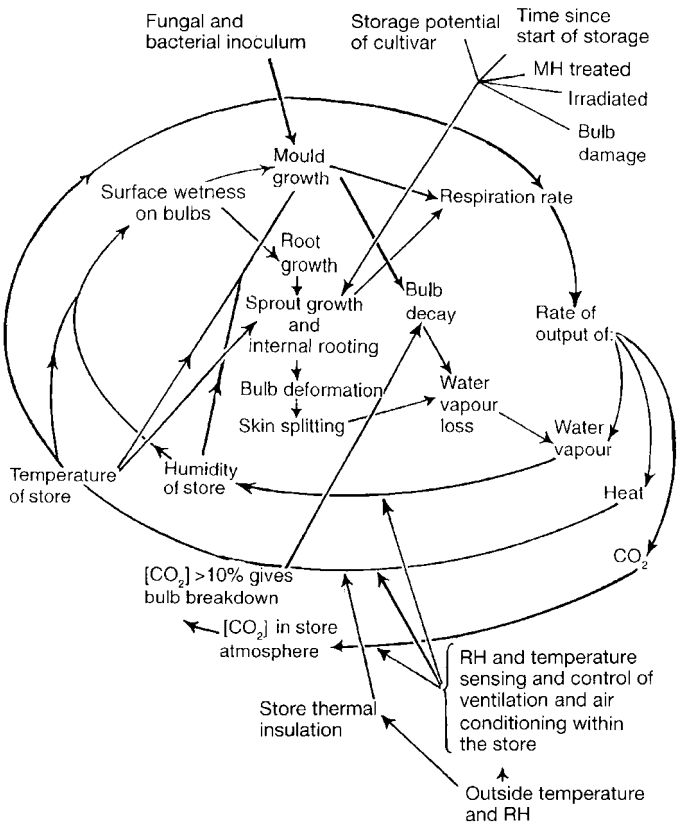


Fig. 7.13. The important factors, processes and interactions within an onion store that can influence bulb sprouting and disease.

and cooled by contact with colder bulbs, the temperature may decline below the dew point of the incoming air and water may condense on the bulbs.

If the base plate of bulbs is wetted, rooting will occur rapidly and this will accelerate sprouting which, as we have seen, will favour increased water loss from bulbs. Therefore, a loss of control, leading to excessive humidity and wetness within the store, can trigger a vicious circle of positive feedback events leading to rapid deterioration of the stored bulbs. High humidity, particularly if combined with high temperatures, favours the spread of pathogens within the store.

In warm storage conditions the rate of deterioration due to pathogens – e.g. black mould, *Aspergillus niger* – usually outweighs the importance of sprouting (Currah and Proctor, 1990). The breakdown of bulbs by rotting will, in itself, probably increase the permeability of the skins to water vapour, and thus increase the rate of transfer of water from bulbs to the store atmosphere. So, various chains of causation are possible, with physical store conditions

influencing biological processes which, in turn, influence the conductivity to water vapour of the onion skins and the heat output of the stored bulbs.

These biological changes can feed back and affect the physical conditions in the store. To counter these changes, the internal environment of the store must be monitored by sensors, and heat and water vapour must be removed or introduced as necessary, using heating, refrigeration and the mixing of external air with the air circulating through the stored bulbs. The rate at which heat or water vapour can be added to, or removed from, the bulbs will depend on the temperature and vapour pressure differences between bulb surfaces and the circulating air, and the boundary layer resistance to heat and water vapour transfer. These will depend on the rate of air flow through the bulbs, and the temperature and vapour pressure of, and the rate of exchange with, ventilating air. By mathematically modelling such a complex and interacting system of variables, it is possible to combine information on the processes involved and to design storage systems that optimize storage conditions. This approach has been applied to the design of high-temperature bulk stores in Brazil (de Matos, 1987).

LOW-TEMPERATURE STORAGE The harvesting and curing systems used prior to cold storage are described in Chapter 6. Onion stores can contain bulbs stacked to a depth of 5 m and need load-bearing walls and ducting, plus under-floor ventilation, to force fan-driven, conditioned, ventilating air upwards through the stack of the bulbs at an appropriate rate (see Fig. 7.14).

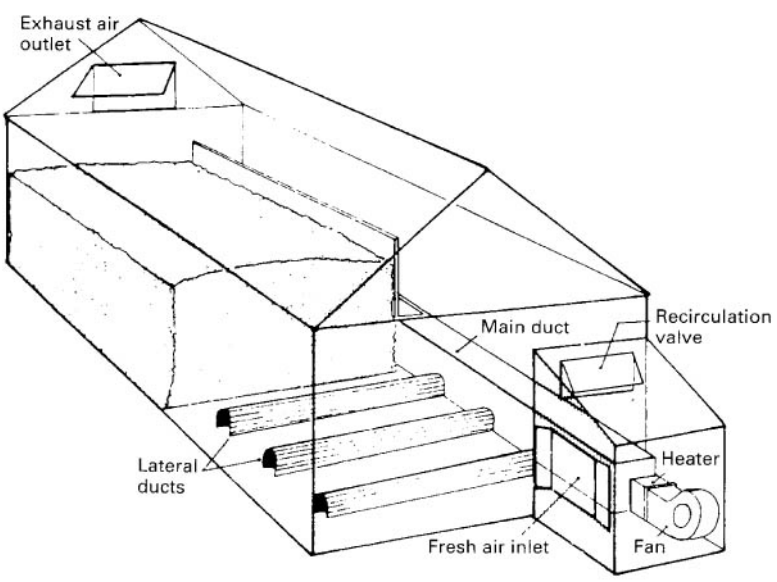


Fig. 7.14. Diagram of a typical bulk onion store (from MAFF, 1978. Courtesy of the Department of Food and Rural Affairs (DEFRA) (UK)).

Sensors for temperature and RH within the stack of bulbs are used to control fans, inlet vents for outside air and heaters, to provide the desired sequence of temperatures, humidities and air flow rates. After the initial drying and curing, the temperature of the bulbs is lowered by about 0.5°C/day by mixing cool air drawn from outside with the air recirculating within the store. Differential thermostats ensure that outside air is drawn into the store only when it is at least 3°C cooler than the internal air. To avoid freezing damage, outside air is not introduced when this is colder than –2°C.

The rate at which cool outside air, with its low water vapour content, is introduced is also controlled to maintain 75–85% RH within the store. Air flow rates of 170 m^3/h/t of onions are blown through the stack during cooling. Using such ambient air cooling, temperatures of 3–5°C can be maintained through the winter in UK stores. For very long-term storage, refrigeration is used to cool the air circulating within the store to –1 to 0°C, again maintaining 75–85% RH. At this RH mould growth on the onion skins is prevented, the onion skins remain fairly flexible and evaporation is slow. Using refrigerated storage at –1 to 0°C, bulbs can be kept without sprouting until June following a September harvest (see Fig. 7.15).

Care is needed when onions are removed from cold storage. They need to be warmed to ambient temperatures slowly, otherwise water will condense on the cold onions from warm air, causing them to attract dirt and dust, and encouraging mould growth and root development. Care must also be taken to avoid the skins becoming brittle because of long exposure to low humidity, as this can result in the loss of skins during subsequent grading and packing (see 'The Mechanical Handling of Onion Bulbs at Harvest, Storage and Packing', above).

HIGH-TEMPERATURE STORAGE Figure 7.15 shows that storage life is longer at 25°C than at 15–20°C. Storage techniques that are economic and suitable for

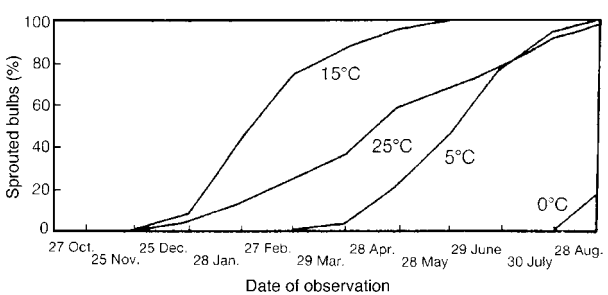


Fig. 7.15. The relationship between time in store and the percentage of bulbs sprouted of onion cv. 'Sapporo-ki' stored at a range of constant temperatures (from Tanaka *et al.,* 1985a. Courtesy of *Research Bulletins Hokkaido National Agricultural Experiment Station*).

tropical and subtropical regions rely on maintaining high temperatures to prolong dormancy. To avoid rotting, the onions must be kept dry and well ventilated. Without forced ventilation the onions must be stored only one to two layers thick, or as strings of bulbs, so that air can circulate freely round the bases of the bulbs. Traditionally, onions were hung in strings from rafters or laid on the floor. Recently, various improved simple stores have been devised where onions are stacked in shallow layers on wire netting shelves (Currah and Proctor, 1990; Brice *et al.*, 1997).

Development work in Brazil has led to the specification of bulk stores in which onions can be stored to a depth of 2 m and force-ventilated by fan-driven air (Currah and Proctor, 1990). Heaters are used to prevent the temperatures falling below 18°C and to keep RH below 75%. The low humidity contrasts with the recommendations for temperate region bulk cold stores and stems from the finding, discussed above, that skin permeability, and therefore bulb water loss, increases at RHs > 75% (see Fig. 7.3b). By including heating, and having the capacity for air flow rates of 2.5 m^3/min/m^3, these stores have been designed to cure the onions as they are loaded into the store, layer by layer.

CONTROLLED-ATMOSPHERE STORAGE Storing onion bulbs in modified atmospheres with elevated carbon dioxide levels and low oxygen levels can prolong dormancy and extend storage life (Gubb and MacTavish, 2002). For example, the Japanese cultivar 'Momiji No. 3' kept for 4 months under ambient storage, 8 months under ambient atmosphere at 1°C or for 12 months with 1% oxygen and 1% carbon dioxide at 1°C (Tanaka *et al.*, 1996). Researchers have found extended storage using such modified atmospheres for both 'storage'-type onions (Adamiki and Kepka, 1974) and short-dormant types. Sweet 'Vidalia' onion quality was best preserved by an atmosphere of 3% oxygen and 5% carbon dioxide at 1 or 5°C (Smittle, 1988).

Recent research has focused on using very low oxygen concentrations. Oxygen levels of 1% in a store maintained at 2°C inhibited weight loss, respiration and sprouting compared with 21% oxygen in the northern European long-storing cv. 'Sherpa' (Praeger *et al.*, 2003). Low oxygen resulted in higher concentrations of water-soluble carbohydrates after long-term storage due to less breakdown of fructans (Ernst *et al.*, 2003); 0.5% oxygen gave similar results but somewhat faster sprouting in spring. Accelerated softening, putrid odours and rots have been reported from oxygen levels < 1% (Gubb and MacTavish, 2002). In adequate oxygen concentrations elevated carbon dioxide levels (10% or more) can cause internal breakdown of cold-stored bulbs (Adamiki and Kepka, 1974; Komochi, 1990). This observation gave a clue to the causes of watery scale disorders in onion bulbs (see following section).

Ethylene gas at 100 ppm (115 mg/m^3) in the store atmosphere prevents sprout elongation within bulbs and hence extends the storage life of onion bulbs, and has been permitted for use in onion stores in the UK (http://www.restrain.uk.com). These low levels of ethylene present no hazard

for store operatives, unlike low-oxygen stores. Ethylene, being a gas, reaches all bulbs in a store uniformly. Once removed from store the ethylene diffuses out of the bulbs within 3 days leaving no residue, unlike maleic hydrazide (MH). As a result, although shelf-life after removal from store is better than for untreated bulbs, it not as good as for MH-treated bulbs. Since there is increasing demand from supermarkets and consumers for produce to be free of residues from applied chemicals, this technique is being rapidly adopted for sprouting control in onion stores.

However, for onions destined for long periods of transport after removal from store, MH is likely to remain useful since the ripening- and senescence-inducing effects of ethylene on other fruits and vegetables make it unlikely that it will be acceptable for use in sprout suppression in onions on ships carrying produce exports. As yet there are scant scientific data reported on ethylene and onion storage. The optimum concentrations of ethylene have not been reported, although 10 μl/l was very effective in inhibiting sprout leaf growth in dormant bulbs stored at 3^0C (Bufler, in press, b). Effects on bulb quality have also yet to be established, although first reports indicate that ethylene prevents the increase in pungency with time in storage but does not prevent the decrease in fructan content and increase in fructose (Bufler, in press, b).

Translucent and leathery scale disorders of onion bulbs

During the late 1970s and the 1980s there were widespread reports from northern Europe of bulbs with one or more scales in a broken down and watery state. This was not associated with a causal pathogen, and the increased prevalence of the disorder coincided with harvesting methods changing to involve mechanical handling, artificial curing and bulk storage. New cultivars with strong, thick skins suited to mechanical harvesting and bulk storage may also have been a factor.

The problem was particularly serious in Norway, and research there established that the symptoms could be induced by submerging bulbs in water for 1–2 days, or by sealing the necks of bulbs with vaseline, both treatments that restrict gas exchange and which lead to internal carbon dioxide levels above 13% (Hoftun, 1993). High internal carbon dioxide is considered the primary cause of watery scale, and this has been termed the 'choke theory' for watery scale.

Further studies showed in detail how such symptoms can arise (Solberg, 1997). Solberg divided watery scale disorders into leathery scales (LS) – which appear as thick, dark, moist scales between the dry outer skin and the inner fleshy scales – and translucent scales (TS), which are water-soaked but firm, fleshy scales occurring initially in the middle or upper parts of outer fleshy scales. The symptoms become more severe after long storage, a tart smell and grey or bright green colours can develop and symptoms can spread to the

whole bulb. Leathery scales can be seen in the field late in the growing season and weak symptoms may disappear during warm-air curing. A slight rise in pH to 6.4 from the normal 5.9 in fleshy scales is first observed, a feature associated with excess carbon dioxide toxicity in plants. Later, the pH declines to 4.1 and ethanol levels increase. The electrical conductivity of the tissues increases as the disorder develops, a characteristic of tissues with membrane leakage and breakdown.

Oxygen permeabilities of dry scales and the epidermis of fleshy scales were 11×10^{-6} and 6.8×10^{-6} cm/s/atm., respectively, lower than the permeability needed to supply respiring fleshy scales, but the permeability of the neck and base (10.8 and 1.9×10^{-4} cm/s/atm., respectively) were much higher, indicating that the neck was the important path for respiratory gas exchange and that there could be negligible radial gas exchange through onion skin and epidermal layers into the bulbs. Blocking the neck by clamping or wetting reduced its oxygen permeability by a factor of four.

Mechanical treatments likely to simulate events during harvesting and curing could cause internal carbon dioxide to reach damaging concentrations within bulbs. Dropping onions on to a hard surface caused a 4% rise in internal carbon dioxide, through increased respiration rate and therefore carbon dioxide production (see Fig. 7.12). Pressure on necks by tying restricted oxygen permeability, leading to a 4% rise in carbon dioxide. A combination of these two treatments led to internal carbon dioxide levels likely to cause damage. Pressure on the necks of onions in a bin from overlying bulbs was observed in about 5% of onions. This could restrict gas exchange in such bulbs and may explain why some show symptoms and others do not.

Field experiments showed that late harvesting, high drying temperatures and long duration of drying give high internal carbon dioxide levels and the high occurrence of translucent scales. Yoo *et al.* (1997) reported higher internal carbon dioxide levels in stored bulbs and lower internal gas volumes with increasing temperature (see Fig. 7.8). They speculated that the lower gas volumes in the neck at warm temperatures could restrict gas exchange and partly explain the greater internal carbon dioxide levels they observed at high temperatures in situations where respiration was not increasing with temperature (see Figs 7.8b, c). In uncured onions straight after harvest a high drying temperature is likely to be associated with a high respiration rate, leading to high internal carbon dioxide levels. Late harvesting is likely to be associated with more moisture on the necks and more collapsed necks, both of which will lower gas permeability compared with conditions at an earlier harvest. Survey data showed that the occurrence of these disorders was associated with years of high rainfall and humidity at harvesting and curing time.

Recommendations for avoidance of these disorders included: (i) early harvesting (not later than 50–80% leaf-fall); (ii) gentle handling of the onions; (iii) avoidance of wet harvesting conditions; (iv) drying in boxes rather than in deep piles to avoid pressure on the onion neck; and (v) drying temperatures

< 25°C (Solberg, 1997). Curing temperatures of above 25°C (e.g. 27°C) have been recommended where dark-coloured skins are desired (see 'The Curing of Bulb Skins', above), and there might be some conflict of requirement here.

GARLIC DORMANCY AND STORAGE

Dormancy has been studied in both Japanese (Takagi, 1990) and Californian (Mann and Lewis, 1956) strains of garlic. The clones studied from both these temperate regions show many similarities to onion bulbs as regards the physiology of dormancy. Clones differ considerably in their innate duration of dormancy, as measured by the time to sprouting, either in storage or after planting.

As with onion, the garlic bulb passes through successive phases, each with a different response to temperature. While the bulb is still immature and growing and soon after maturity, the depth of dormancy, as measured by days to sprouting after planting, is decreased by temperatures of 35°C, as with onion. When the bulbs are mature, dormancy is most rapidly depleted by storage at 5–10°C and prolonged by both lower and higher temperatures. Between 15 and 30°C, time to sprouting increases progressively with temperature. Respiration rates of bulbs, measured soon after maturity, are more rapid at 5, 10, and 15 than at 0 or 20°C. So, as with onion, there is a prolongation of dormancy, and suppression of metabolic activity by moderately warm storage. The optimum temperatures for sprouting in garlic (5–10°C) are about 5°C lower than with onion.

In the Japanese cv. 'Yamagata', which is not innately a long-storing strain, leaf initiation ceases as the bulb matures. It does not resume, even in cloves planted in ideal conditions, for 3 weeks or so. So, around the time of foliage collapse, there is a period of 'rest' during which growth at the shoot apex ceases, as with onion. At this stage, the time from clove planting to visible sprouting is maximal. This interval decreases the longer the bulbs are stored. Leaf initiation resumes within stored bulbs, and respiration rates increase slowly, so there is a gradual emergence from the state of innate rest and dormancy. Ultimately, the response of sprouting to storage temperature changes, so that in cloves about to sprout, temperatures of 20–30°C cease to suppress sprouting.

Root appearance, following planting cloves on moist sand, takes only a few days, typically just a quarter of the time for visible sprouts to emerge. So, as with onion, rooting precedes sprouting. As with sprouting, rooting is fastest after storage at 5–10°C. Immersing garlic cloves in benzyl adenine solutions before planting greatly accelerates sprouting, indicating a role of cytokinins in breaking dormancy, another feature in common with onion bulbs.

In practice, garlic bulbs are normally stored at ambient temperatures. Experiments have shown that the optimum temperature for prolonged storage is –1 to –3°C. Bulbs sprout most rapidly in storage at 5–10°C. They store

satisfactorily at 20–30°C, but moisture loss and shrinkage are rapid at these higher temperatures. It is critical to keep relative humidities during storage below 70% to avoid the growth of surface moulds and prevent root emergence. As with onion, sprouting can be prevented by spraying plants with maleic hydrazide while bulbs are maturing but with leaves still green, or by treating bulbs with gamma radiation after harvest.

LEEK STORAGE

Research in Scandinavia has investigated how autumn-harvested leeks can be stored through the winter (Hoftun, 1978a, b). More recent research on the storage of leeks harvested in the early spring in the UK has broadly confirmed the Scandinavian findings on the best regimes for preserving high-quality leeks.

In contrast to onion and garlic bulbs, the pseudostem and lower part of the green leaves, which are normally harvested from leek, are not naturally dormant. Table 7.2 and Fig. 7.16 show that the respiration rate of leeks increases progressively and rapidly as temperature increases. The rate of deterioration in store shows a parallel and rapid increase with temperature.

During storage, leeks lose weight by evaporation, by respiration and because the leaves, particularly the green parts, yellow and must be trimmed

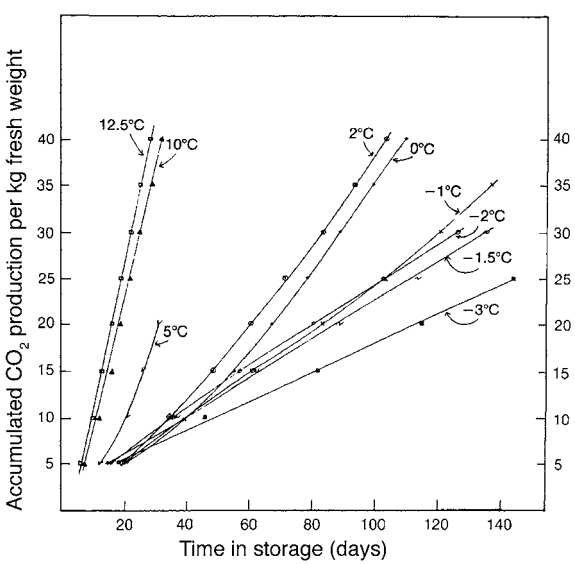


Fig. 7.16. The accumulated CO_2 production of leeks after storage at a range of constant temperatures (from Hoftun, 1978a. Courtesy of *Meldinger fra Norges Landbrukhogskole*).

before the leeks are marketed. Both the weight loss by trimming and the decline in the percentage of leeks in the top-quality grades are closely correlated with the amount of CO_2 respired. High quality is equated with the presence of a bright green, fresh-looking 'flag' of leaf blades persisting at the top of the trimmed leek. Per kilogram of leeks, every gram of CO_2 respired equates with a loss of 1.4% of the crop weight by trimming.

It is not surprising, therefore, that storage life is prolonged by treatments that minimize respiration. These are of low temperature, plus elevated carbon dioxide and lowered oxygen concentrations in the store atmosphere. To minimize evaporative losses, relative humidities should be kept at 95% or above. Leeks for storage should be of high quality and with the minimum of damage on entering the store. They must be stacked in crates with the pseudostems upright, otherwise they will bend during storage, probably due to gravitropic growth.

The optimum temperature for storage is –1°C. Freezing damage, characterized by a softening of the tissue on removal from store, can occur at –2°C, and this damage increases the longer the leeks are kept in store. Storage at –3°C rapidly causes freezing injury. The damaging effects of freezing are minimized if the temperature of the leeks is raised slowly after removal from store, for example, by placing them at 5°C. Deterioration is also rapid at temperatures above 0°C. For example, with the Norwegian cv. 'Sommar' after just 33 days of storage, the weights of trimmed leek, as a percentage of the weights put into store, were 98, 65, 46 and 42 at 0, 5, 10 and 12.5°C, respectively (Hoftun, 1978a). The quality of the trimmed leeks also declined with temperature.

So, long-term storage needs temperatures of –1 to 0°C. At these temperatures, after 4 months of storage, about 40% of the weight of leeks originally put into store was marketable. Experiments in the UK have shown that a temperature of 0–1°C can maintain more than 80% of leeks at a high market quality for up to about 9 weeks.

Quite dramatic increases in leek storage life can be achieved by using controlled atmospheres. Carbon dioxide levels of around 10% are optimal (Fig. 7.17). After 5 months of storage at 0°C under CO_2:O_2 percentages of 0.5:20.5, 10:10 or 10:1, the respective percentage weight losses following trimming were 72, 21 and 17 in the experiments of Fig. 7.17. After 8 months' storage the respective losses were 99, 62 and 39%. As can be seen from Fig. 7.17, when the CO_2 concentration is low, the rate of deterioration is greatly slowed by reducing the oxygen concentration in the store atmosphere. At 10% CO_2, the benefits of low oxygen levels are less; below 10% O_2, respiration rates decline as O_2 concentration declines, and the decrease in respiration is highly correlated with increases in the percentage of top-quality leeks emerging from 5 months' storage.

Elevated CO_2 concentrations and reduced O_2 also conserve chlorophyll in the flag leaf during storage, resulting in greener, fresher-looking leeks at the end. Experiments in the UK and Finland have confirmed that the benefits of cold storage are much enhanced by CO_2 concentrations of around 10%. In

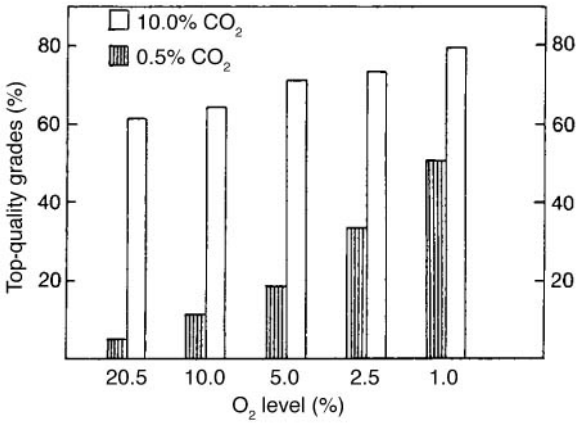


Fig. 7.17. Percentages of leeks cv. 'Acquisition' in top-quality grades, based on weight at input, after 5 months' storage at 0°C in different O_2 concentrations in 0.5 or 10% CO_2 (averages of 3 years' data) (from Hoftun, 1978b. Courtesy of *Meldinger fra Norges Landbrukhogskole*).

prolonged storage at 15% CO_2, some internal damage to leeks occurs, and storage at 20% CO_2 causes the tissues to collapse.

In terms of practical conclusions, these trials have shown that it is possible to maintain trimmed leeks at a high quality for about 2 months when they are stored upright at –1 to 0°C and at 95% RH. This duration of storage can probably be approximately doubled by using, in addition, a near-optimal controlled atmosphere, like 10% CO_2 and 1% O_2. Leeks should be cooled down to the storage temperature as soon as possible after harvest. They should be slowly warmed up after storage, using a temperature around 5°C, and should be kept at low temperature and high RH during marketing.

GREEN ONION STORAGE

Green, leafy onions cut for fresh salad use are at the opposite end of the vegetable storability spectrum to the naturally dormant onion, shallot or garlic bulb, being a highly perishable commodity with much in common with other leafy salad vegetables. For example, the data of Hong and Kim (2001) show that at 20°C green *A. fistulosum* respired approximately 20 times faster than dormant bulb onions, while at 10°C the difference was a factor of eight and at 0°C a factor of seven.

After harvesting, green onions are prone to rapid water loss leading to limpness and loss of turgor. They have a high respiration rate typical of young, growing plants and therefore internal reserves of carbohydrate decline rapidly.

With time, green leaves senesce and yellow, cut ends of tissues brown, microbial populations on the tissue increase and nutritional quality – in terms of sugars, vitamins and flavour – declines. Such changes are common to all fresh, leafy vegetables. Problems specific to cut alliums include: (i) extension of the roots on those root-trimmed to leave the stem base intact; (ii) geotropic curvature if the plants are stacked horizontally; and (iii) if the stem base is trimmed off leaving just pseudostem tissue, the leaf sheaths may extend after trimming, the inner ones growing more than the outer to give an unsightly effect known as 'telescoping' (Cantwell *et al.*, 2001). Products thus trimmed, or processed to a greater extent – for example, chopped into leaf 'rings' 1 cm long (Fan *et al.*, 2003) or shredded and mixed with other leaves in ready-to-eat mixed salads (Vieira *et al.*, 2003), both for retail or sale to food service companies – represent an expanding market for green onion products.

The time for which such produce can be maintained acceptably fresh can be extended by storage at low temperatures, high humidity (> 95%) and in an atmosphere of low oxygen and high carbon dioxide concentration. A range of packaging films exist which vary in their permeability to oxygen and carbon dioxide. Within a package that is fairly impermeable to these gases, carbon dioxide concentration initially increases and oxygen decreases as the product respires. Depending on both the relative permeability of the packaging film to oxygen and carbon dioxide and the respiration rate of the product, a modified atmosphere can be established within the package that prolongs storage life (Fonseca *et al.*, 2000). Establishment of the desired atmosphere can be aided by initially filling the package with the desired gas mixture. Currently, green alliums are packaged in films resulting in < 1% oxygen and 8–10% carbon dioxide (Hong *et al.*, 2000).

The benefits of cold temperatures are well known, and green alliums have a shelf-life of up to 4 weeks at 0°C (Hruschka, 1974). However, the cleaned produce frequently has to be kept at 4–5°C, and in these temperatures shelf-life can be extended by modified atmospheres. Hong *et al.* (2000) reported that trimmed green hybrid (*A. cepa* × *A. fistulosum*) onions had a shelf-life of no more than 7 days at 10°C, regardless of storage atmosphere. At 5°C an atmosphere of 0.1–0.2% oxygen with 7.5–9.0% carbon dioxide slowed leaf discoloration, prevented geotropic curvature, prolonged high visual quality and, in onions with an intact base plate, kept root extension to negligible levels over 21 days. This treatment reduced, but did not stop, inner leaf extension (telescoping) in trimmed onions. Very similar results were given by 0.2% oxygen alone, but in 2% oxygen responses were little different to those in normal air. With modified atmospheres good quality was maintained for more than 2 weeks at 5°C. At 0°C high visual quality and zero curvature was maintained for 3 weeks, but by then a low-oxygen atmosphere in addition was more preventive of leaf discoloration.

In a subsequent study, extension growth of cut onions was reduced by dipping 4 cm of the basal end in hot water at 52.5 or 55°C for 4 or 2 min, respectively (Cantwell *et al.*, 2001). After 10 days at 5°C the extension of heat-

treated onions was less than 5 mm, whereas non-dipped onions had grown by an unacceptable 10–20 mm. The heat treatment increased respiration rate above control levels by about 40% but did not reduce visual quality or shelf-life.

To reduce the microbial population, minimally-processed products like green onions are washed in chlorinated water, e.g. 50 N mg/l NaOCl (sodium hypochlorite). Hot water dips also reduced the microbial population and, by adding sodium hypochlorite to the hot water at rates of up to 200 mg/l, the plate count of aerobic microorganisms was reduced 200-fold compared with an unheated wash in hypochlorite (Cantwell *et al.*, 2001).

Microbial contamination can also be reduced by gamma radiation. Green onions trimmed into 1 cm leaf rings, washed in 100 mg/l sodium hypochlorite and subjected to gamma radiation at 1 kGy showed a 300-fold reduction in microbial count immediately after treatment compared with non-irradiated material and a sixfold reduction after 14 days at 3°C, along with improved visual quality. Doses of 2 and 3 kGy caused membrane damage and resulted in loss of aroma and visual quality, although the microbial count was below the detectable limit throughout 14 days (Fan *et al.*, 2003).

Green *A. fistulosum* washed, trimmed and cut into 10 cm lengths showed a response of respiration rate to oxygen concentration that could be described by the Michaelis-Menten equation from enzyme kinetics (Hong and Kim, 2001):

$$R = V_m [O_2]/(K_M + [O_2]) \qquad \text{(Eqn 7.1)}$$

where
R = respiration rate
$[O_2]$ = oxygen concentration of atmosphere
V_m = maximum respiration rate
$K_M = [O_2]$ at half maximal respiration rate ($0.5V_m$), the Michaelis constant K_M had an average value of 1.67% oxygen.

Maximum respiration rate, V_m, increased with temperature, approximately threefold for every 10°C between zero and 20°C. At 10°C it had a mean value of 30 ml/kg/h of oxygen uptake or carbon dioxide output. Other reports have given a V_m of 43 ml/kg/h and a K_M of 1.24 oxygen for green *A. fistulosum* and a V_m at 10°C of 49 ml/kg/h and K_M of 0.46% oxygen for green *Allium wakegi* (Hong and Kim, 2001).

The relationship between maximum respiration rate and temperature for green onions followed the Arrhenius equation over the range 0–20°C (Hong and Kim, 2001). At 0, 10 and 20°C the respiratory quotient (carbon dioxide output:oxygen uptake) remained unity until oxygen concentration decreased below 1%, after which it began to increase sharply, indicating a shift from aerobic to anaerobic respiration. This leads to the accumulation of ethanol and acetaldehyde, which are toxic to cells and cause off-flavours in fresh produce. These respiration parameters should be useful for modelling expected respiration and designing appropriate modified-atmosphere packaging for fresh-cut green onions (Hong and Kim, 2001).

8

Biochemistry, Health Benefits and Food Science of Alliums

This chapter reviews aspects of biochemistry that are special to alliums, all of which are relevant to their properties as foods, both raw and processed, and also to their well-known health benefits. Subjects reviewed are the biochemistry of the flavour compounds, aspects of carbohydrate biochemistry and, thirdly, the flavanoids responsible, among other things, for the colour of onion bulbs. The evidence for health benefits from allium vegetables is then discussed. The chapter ends with a brief consideration of the use of allium vegetables for various processed foods and for making extracts for flavouring or medicines.

THE BIOCHEMISTRY OF FLAVOUR

Allium vegetables are grown primarily for their distinct flavours. The nature, biosynthesis and properties of the compounds that give rise to flavours have been slowly uncovered by research spanning from the late 1940s to the present day. The chemistry of allium flavour is complex, because the sulfur-containing compounds responsible for flavour are labile and reactive. They are released only when cells are damaged by slicing or crushing.

This sets in train a series of reactions starting with the release of an enzyme, alliinase, present only in the vacuoles of undamaged cells, giving it access to flavourless precursors that are stored in vesicles in the cytoplasm. The alliinase converts the precursors to reactive and strongly flavoured thiosulfinates that are the primary flavour compounds. The quantity and nature of the thiosulfinates released depends in part on how thoroughly the tissue is macerated and for how long the enzyme can act before being destroyed by cooking or processing.

What compounds are formed from thiosulfinates depend on cooking or extraction conditions. More than 80 different compounds have been characterized, formed by the interaction among the initial thiosulfinates and the subsequent cascade of reaction products in fresh, and also steam-distilled, extracts of alliums. These substances include polysulfides, thiosulfonates and compounds with an S in ring structures, e.g. dithiins. The organic chemistry of

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allium flavour compounds was reviewed by Block (1992), and subsequent papers continue to develop the subject (Block *et al.*, 1997). The biochemistry and physiology of the flavour compounds were reviewed by Lancaster and Boland (1990), Randle and Lancaster (2002) and Jones *et al.* (2004).

Garlic and onion were known to have curative properties in many ancient folk medical traditions. To a large extent, but not exclusively, these remedial properties are a result of the flavour compounds. Hence, there has been a strong motivation for researchers to characterize the active compounds and their pharmacological properties. Garlic is one of the best-studied medicinal plants (Koch and Lawson, 1996; Keusgen, 2002), while work on the health benefits of onion is somewhat less advanced (Griffiths *et al.*, 2002). References to the original papers describing the work outlined here can be found in these various review articles.

Precursors of flavour compounds

In alliums most of the sulfur is in the form of various non-protein amino acids, which include the precursors of the volatile flavour compounds. These precursors are odourless, non-volatile amino acids of the general name S-alk(en)yl cysteine sulfoxides (ACSOs). The general structure of the ACSOs is:

O
↑
R-S-CH_2-CH(NH_2)COOH; the group to the right of the R group is the -L-cysteine sulfoxide group.

The group R can include:

- CH_3- called (+)-*S* methyl (MSO)
- CH_3-CH_2-CH_2- called (+)-*S* propyl (PSO)
- CH_3-CH = CH- called *trans* (+)-*S*-(1-propenyl) (1-PECSO)
- CH_2 = CH-CH- called (+)-*S*-(2-propenyl) (2-PECSO)

Compound 4, from garlic, was the first to be isolated and is commonly called alliin or S-allyl-cysteine sulfoxide.

Species of allium differ in their R groups and the relative proportions of their L-cysteine sulfoxides (see Table 8.1). In garlic, 2-PECSO is predominant and in onion 1-PECSO, and these two precursors dominate the flavour biochemistry of their respective crops. The sulfoxide bond is asymmetric and gives rise to optical isomers, but the naturally occurring compounds are all of the (+) isomers. A large fraction of the ACSOs (50% or more) are linked to a glutamic acid group to form γ-glutamyl ACSOs within the plant (see Fig. 8.1). γ-glutamyl-linked ACSO does not react with alliinase flavour enzyme and does not therefore contribute to flavour on crushing. The g-glutamyl group must first be removed by a g-glutamyl transpeptidase-mediated reaction to release the free ACSO for it to enter the flavour-releasing reactions.

Table 8.1. Flavour precursors (cysteine sulfoxides) detected in edible alliums and their relative amounts (based on more detailed information from Lancaster and Boland, 1990, Table 1).

	Flavour precursor			
Species	S-methyl (MSO)	S-propyl (PSO)	S-(1-propenyl) (1-PECSO)	S-(2-propenyl) (2-PECSO)
Onion, *A. cepa*	+	+ +	+ + +	0
Shallot, *A. cepa* var. *ascalonicum*	+ +	+ +	+	0
Rakkyo, *A. chinense*	+ +	+	+ +	0
Japanese bunching onion, *A. fistulosum*	+	+ +	+ +	0
Chives, *A. schoenoprasum*	+	+	+ +	0
Leek, *A. ampeloprasum*	+ +	+ +	+	0
Great-headed garlic, *A. ampeloprasum*	+ +	+	0	+ + +
Garlic, *A. sativum*	+ +	+	0	+ + +
Chinese chives, *A. tuberosum*	+ +	+	+	+ + +

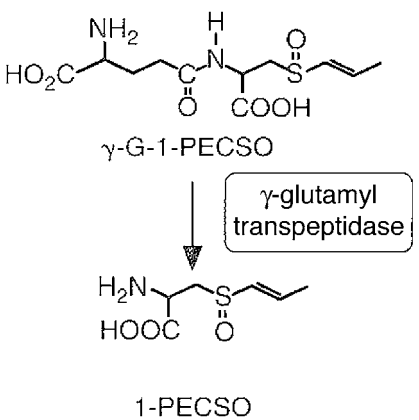


Fig. 8.1. γ-glutamyl-trans-(+)-s-(1-propenyl)-cysteine sulfoxide (upper), which forms approximately 50% of the potential flavour precursors in onion bulbs. As shown, it is split from the γ-glutamyl group by the γ-glutamyl transpeptidase enzyme to produce trans-(+)-s-(1-propenyl)-cysteine sulfoxide (abbreviated to 1-PECSO) (lower). This can be converted to flavour volatiles by the alliinase enzyme reaction of Fig. 8.2 (part of Fig.14.4 of Randle and Lancaster, 2002).

Enzyme reactions in flavour generation

When fresh tissue is damaged, flavour precursors react under the control of alliinase (S-alk(en)yl-L-cysteine sulphoxide lyase) to release the highly reactive sulfenic acids, plus ammonia and pyruvate, as illustrated in Fig. 8.2. The enzyme is confined to the cell vacuole, whereas the flavour precursors are confined to the cytoplasm, probably within small vesicles associated with their presence in the cell. Hence, the enzyme has access to the precursors only when cells are disrupted. This explains why onion bulbs boiled whole, without previously damaging the tissue, lack flavour, since the enzyme will be destroyed before having access to the flavour precursors. In garlic bulbs the alliinase is confined to the bundle sheath cells that surround the vascular bundles within the cloves.

The enzyme alliinase

Some details of the alliinase reaction are shown in Fig. 8.2. Piridoxal-5′-phosphate is an essential cofactor that is tightly bound to the enzyme protein in a 1:1 ratio. Alliinase is a glycoprotein with approximately 4.6% of its weight comprising mannose-rich carbohydrate. Alliinase comprises about 6% of the soluble protein of onion bulb tissue and exists in the cell vacuole both as single units (monomers) or linked as several enzyme units in multimers, in association with mannose-specific lectins. The amino acid sequence of several alliinases has been established from the DNA sequence of the corresponding

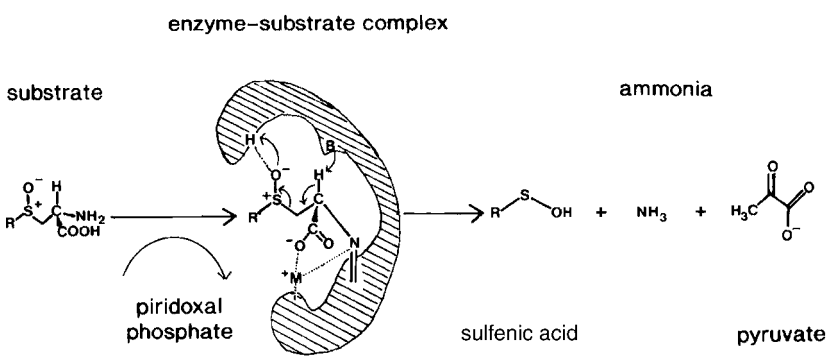


Fig. 8.2. Catalysis of the conversion of flavour precursors to highly reactive sulfenic acids by the alliinase enzyme. The group R depends on species (see Table 8.1). Piridoxal phosphate acts on the precursor so that it forms an enzyme–substrate complex involving electrostatic attraction of the substrate for a metal ion (M^+). A basic group on the enzyme then removes a hydrogen ion (H^+) from the substrate, triggering its collapse to release a sulfenic acid, ammonia and pyruvate (redrawn from Block, 1985).

genes. The enzyme contains a chain of 445 amino acids, with the pyridoxal phosphate binding with a lysine unit at position 285. A tryptophan unit at position 182 is essential for activity. Several forms of the enzyme may exist that may differ in affinity for the varying ACSOs.

Volatile flavour compounds

The highly reactive sulfenic acids, once released, proceed to undergo rearrangement and inter-reactions to produce a wide range of volatile, strongly smelling products. The 1-propenyl sulfenic acid (1-PECSO) produced in onions rapidly enters a reaction catalysed by the recently discovered enzyme lachrymatory factor synthase (Imai *et al.*, 2002) to form the tear-inducing thiopropanal S-oxide (see Fig. 8.3). In garlic alliinase releases 2-PECSO, two of which spontaneously combine to form the thiosulfinate allicin, which gives fresh garlic its characteristic smell.

$$\underset{\text{Alliin}}{2\,CH_2{=}CH\text{-}CH_2\text{-}\overset{\overset{\displaystyle O}{\uparrow}}{S}\text{-}CH_2(NH_2)COOH} \xrightarrow{\text{alliinase}} \underset{\text{Allicin}}{CH_2{=}CH\text{-}CH_2\text{-}\overset{\overset{\displaystyle O}{\uparrow}}{S}\text{-}S\text{-}CH_2\text{-}CH{=}CH_2} + \text{ammonia} + \text{pyruvate}$$

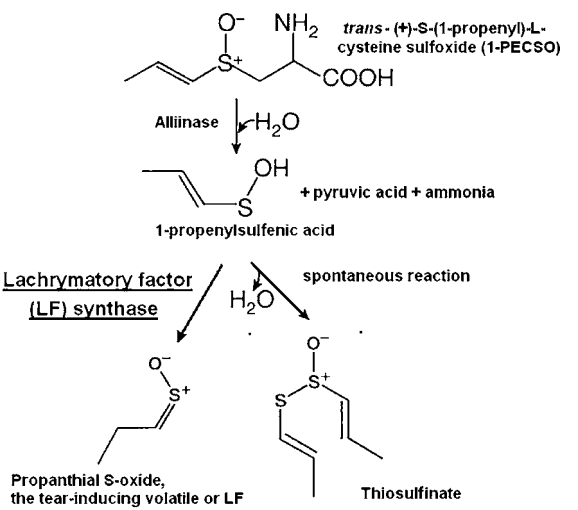


Fig. 8.3. The involvement of the enzyme 'lachrymatory factor synthase' in the production of the tear-inducing volatile propanthial S-oxide (the lachrymatory factor (LF)) when onion bulbs are sliced. Previously, LF was believed to be formed spontaneously following the action of alliinase, but the enzyme LF synthase, alliinase and PECSO must all be present for LF to be produced (redrawn from Imai *et al.*, 2002).

Allicin, other thiosulfinates and the lachrymatory factor of onion are all highly reactive and can undergo further rearrangement and combination with themselves, their reaction products and with sulfenic acids to produce, among others:

1. Thiosulfinates	O ↑ R-S-S-R′
2. Thiosulfonates	O ↑ R-S-S-R′ ↓ O
3. Monosulfides	R-S-R′
4. Disulfides	R-S-S-R′
5. Trisulfides	R-S-S-S-R′

Here, R and R′ can be the same or any pair of R groups listed above that exist as ACSO precursors in an allium species.

More complex structures, including S and C atoms in heterocyclic rings, have also been identified. The actual composition of the reaction mixture depends on the initial concentration and ratio of the R groups forming sulfenic acids, the temperature – hence the difference in flavour of fresh and cooked alliums – the polarity of solvents surrounding the reactants and the pH. The first technique used to extract garlic volatiles was steam distillation, and under these conditions diallyl disulfide (DADS) accumulates. This method is still widely used to produce garlic extracts for encapsulation. More than 80 volatile compounds have been identified in fresh and steam-distilled extracts of alliums. Notable compounds include, from garlic, ajoene (see Fig. 8.4), which has a stronger anti-thrombotic effect than aspirin and which forms from allicin in ethanolic solutions; and, from onions, cepaenes of similar structure to ajoene (see Fig. 8.4), and these too have potent anti-thrombotic properties.

The biosynthesis of flavour precursors

Sulfur enters the plant as sulfate from the soil solution, and after being absorbed by a high sulfate-affinity transporter protein it moves in the vascular tissue to the leaves and there undergoes sequential enzymic reduction and transfer reactions to be incorporated in the amino acid cysteine. Cysteine may then combine with glutamic acid and then glycine to form glutathione. There

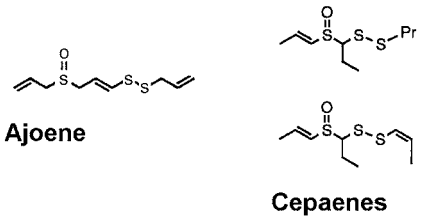


Fig. 8.4. Compounds with powerful anti-thrombotic activity isolated from extracts of garlic and onion. (a) Ajoene, which is found in garlic extracts (from Block, 1985) and (b) two of the many cepaenes found in onion extracts (from Block *et al.*, 1997; diagrams of the chemical structures kindly provided by Professor Eric Block).

is evidence for two possible biosynthetic pathways to form the ACSO flavour of precursors in onion (Griffiths *et al.*, 2002; Jones *et al.*, 2004). These reactions involve the addition of the R side chain to the cysteine group, followed by its modification if necessary to a propenyl group (for 1-PECSO and 2-PECSO), followed by oxidation of S to form the sulfoxide. There is disputed evidence that these reactions all occur with the cysteine and, ultimately, the ACSO group attached to a γ-glutamate group.

Factors affecting flavour compounds

Flavour strength in onions varies with genotype and environment (Randle and Lancaster, 2002). Smaller quantities of volatile S compounds are produced from the mild-flavoured cultivars like 'Sweet Spanish' than from more pungent ones like 'Red Creole'. Within cultivars there is considerable variation in content of the flavour compounds, and cultivar assessment must be based on samples of ten or more bulbs.

Flavour is a heritable genetic characteristic that can respond to selection. Flavour strength in onions is also subject to environmental control. Experiments in solution culture have shown that with a low concentration of sulfate in the nutrient solution, healthy plants can be produced that lack flavour precursors. At the opposite extreme, with increasing S supply a saturation point is reached after which the additional sulfate does not increase pungency. Sulfur deficiency changes the relative proportions of the different ACSOs, with a higher proportion of methyl and propyl CSOs under S deficiency rather than the 1-propenyl CSO that dominates under a plentiful S supply. As applied sulfate levels increase, a greater proportion of S remains in the form of sulfate within the plant. Sandy soils in some localities are low in sulfate, which is easily leached from such soils, and very mild-flavoured onions can be grown there. For example, the light soils of the Vidalia district of Georgia, USA are famous for producing mild, sweet, 'Grano'-type onions.

Flavour strength in onions increases with temperature; in one study, bulb pungency doubled between 10 and 30°C. Growing onions under dry conditions has been shown to result in a greater pungency than under plentiful irrigation. Flavour compounds increase as N levels increase from low levels, although 1-PECSO reaches a maximum at moderate N. Increasing the selenate level in the growing medium reduces pungency and has an effect similar to sulfur deficiency on the relative ratios of the different ACSOs, i.e. 1-PECSO goes down and MCSO up. As a general rule stress factors, e.g. nutrient imbalance or drought, tend to increase onion pungency, possibly because growth is restricted by stress, thereby allowing the flavour compounds to accumulate to a greater concentration within the plant.

A number of studies have shown that onion bulb pungency tends to increase with storage. Available 1-PECSO and the consequent lachrymatory factor release increases during storage, resulting in a generally harsher flavour. However, other studies have shown cultivars differing in their response of pungency to storage, with some cultivars decreasing in pungency with time. The magnitude of these effects depends on storage temperature.

The measurement of flavour

Various methods have been used to measure onion flavour and pungency. The concentration of total ACSOs within the bulb tissue can be measured and, in some cases, the amounts of the different ACSOs have been measured. Total ACSO concentration gives an indication of the potential for pungent flavour present. A more widely used technique, which is simple and more appropriate for routine analysis, is to measure the quantity of pyruvate released by the alliinase reaction (see Fig. 8.2) following maceration of tissue in water and allowing it to stand for 1 h. The quantity of pyruvate formed can easily be measured and indicates how much ACSO has been degraded by alliinase. An alternative is to use gas chromatography to measure the amount of lachrymatory factor formed after maceration (McCallum *et al.*, 2005c). A novel technology that shows promise is to characterize the flavour of an onion homogenate by the output signal from an electronic nose (Abbey *et al.*, 2004).

Pyruvate production is well correlated with total ACSO content of onions (Crowther *et al.*, 2005). There is an increasing market for mild, sweet onions that are nice to eat raw. Mildness or sweetness is negatively correlated with pyruvate production, and pyruvate < 4 μmol/g fresh weight has been suggested as a permissible quality control maximum in sweet onion production (Crowther *et al.*, 2005). However, taste-panel trials show that the perception of different onion cultivars as 'sweet' and 'likeable' is only partly characterized by the pyruvate score and that other factors, including the texture or crispness, influence taste perception. Pyruvate measurement would be suitable for routine

quality control once the characteristics of a cultivar have been established, but initial evaluations require taste-panel assessment. Interestingly, some cultivars are perceived as 'sweet' although they have quite a high pyruvate score, indicating a high ACSO content. Differences in sugar content could not explain this anomaly (Crowther *et al.*, 2005). This presents the interesting possibility of 'sweet' onions that are likeable raw but which have a high content of the health-promoting substances that derive from ACSOs.

A laboratory-based colorimetric method is routinely used for pyruvate determinations in onion flavour assessment (Crowther *et al.*, 2005). Disposable biosensors for pyruvate concentration in macerated onion juice have been developed (Abayomi *et al.*, 2006). These measure the electrical signal generated by a reaction involving the enzyme pyruvate oxidase immobilized on an electrode surface. The biosensors can be used to assess flavour strength on site rather than in a centralized laboratory and can reduce the time and cost of routine assessments for onion quality control 12-fold.

The biological function of flavour compounds

The flavour precursors give rise to many compounds with strong physiological effects on other organisms (see below); this, and the fact that they are released when cells are damaged, suggests that they are important in chemical defence, both by deterring phytophagous animals (Hile *et al.*, 2004) and by being toxic to invading fungi and bacteria. *In vitro* tests with extracts of onions and garlic have shown them to inhibit the growth of more than 80 species of plant-pathogenic fungi (Fenwick and Hanley, 1985b). Allicin has been tentatively identified as fungicidal or fungistatic against a number of plant-pathogenic fungi, and DADS was active against ten plant pathogenic fungi. Extracts of onions and garlic are insecticidal and have also been shown to be toxic to a number of plant-parasitic nematodes.

The major pests and diseases of alliums tend to be highly adapted to their hosts and to use the characteristic volatiles as signals in locating their hosts, e.g. the onion fly, *Delia antiqua*, the leek moth, *Didromus pulchellus* and sclerotial germination and root invasion by the white rot fungus *Sclerotium cepivorum* (see Chapter 5).

ACSOs and their γ-glutamyl derivatives can amount to 1–5% of the dry weight of allium plants and seeds, and alliinase comprises about 6% of the total soluble protein of onion bulb tissue. These substances probably have an important role for nitrogen, sulfur and carbon turnover, storage and transport within allium plants. The high quantity, vacuolar location and tendency to aggregate in multimers of alliinase are typical features of storage proteins.

CARBOHYDRATE BIOCHEMISTRY

The non-structural carbohydrates of alliums make up much of the dry matter; for example, 60–80% of the dry matter in onion bulbs (Rutherford and Whittle, 1982; Hansen, 1999). The biochemistry of these carbohydrates was reviewed by Darbyshire and Steer (1990), but the subject has developed considerably since then, accompanied by a growing recognition of its importance for human nutrition and for the understanding of the physiology of allium plants. These carbohydrates comprise glucose, fructose, sucrose and fructans. Starch is rare in onions, but does occur in the stem (i.e. baseplate) around vascular bundles and in the primary thickening meristem (see Chapter 2) during sprouting, and also in root cap cells (Ernst and Bufler, 1994).

Fructans are linear and branched polymers of fructose that occur as reserve carbohydrates in about 15% of flowering plant species (Vijn and Smeekens, 1999). The fructans in alliums mostly contain a single sucrose unit (glucose-1 linked to fructose-2), to which are attached chains of 1–2 linked fructose units joined at either the 1-fructose of the original sucrose or the 6-glucose of the original sucrose, or branching from both these points (see Fig. 8.5; Shiomi *et al.*, 2005; Benkeblia and Shiomi, 2006).

The number of linked fructose units, plus the single glucose unit, gives the degree of polymerisation (DP) of the fructan. Fructans of low DP are termed fructo-oligosaccharides and are the type most common in allium vegetables. Onion, shallots, *A. fistulosum*, most leek cultivars and chives contain fructo-oligosaccharides of a DP up to 20, but the shorter the chain length the greater their proportion of the total fructan. Garlic contains large amounts of high-DP fructan (average DP 41) and little fructo-oligosaccharide. Chinese chives and a winter leek cultivar contained both fructo-oligosaccharides and high-DP fructans (Ernst *et al.*, 1998).

The dry matter and soluble carbohydrate content of onion bulbs can vary by a factor of three or so, being only about 7% in some sweet types, but up to about 22% in cultivars grown for dehydration (Sinclair *et al.*, 1995a). The carbohydrate composition differs dramatically between these types. White 'Sweet Spanish', with 7.5% dry matter, contained about 75% of the bulb-soluble carbohydrate as glucose plus fructose, about 18% as sucrose and 7% as fructans (DP 3 or more). The cross cv. 'White Creole' × 'Southport White Globe' contained 17.2% dry matter and had approximately 3, 7 and 90% of the carbohydrates in the above three categories, respectively. Also, the higher the percentage dry matter content the higher the mean DP of the fructans in the bulbs (see Fig. 8.6). The dry matter percentage of onion bulbs is highly correlated with the soluble solids content of juice extracted from them, as measured by refractometer (see Fig. 8.7). The high fructan DP of garlic bulbs correlates with their high dry matter percentage.

Fructan biosynthesis in onions involves first the production of 1-kestose, which is catalysed by sucrose:sucrose 1 – fructosyl transferase (SST). As its

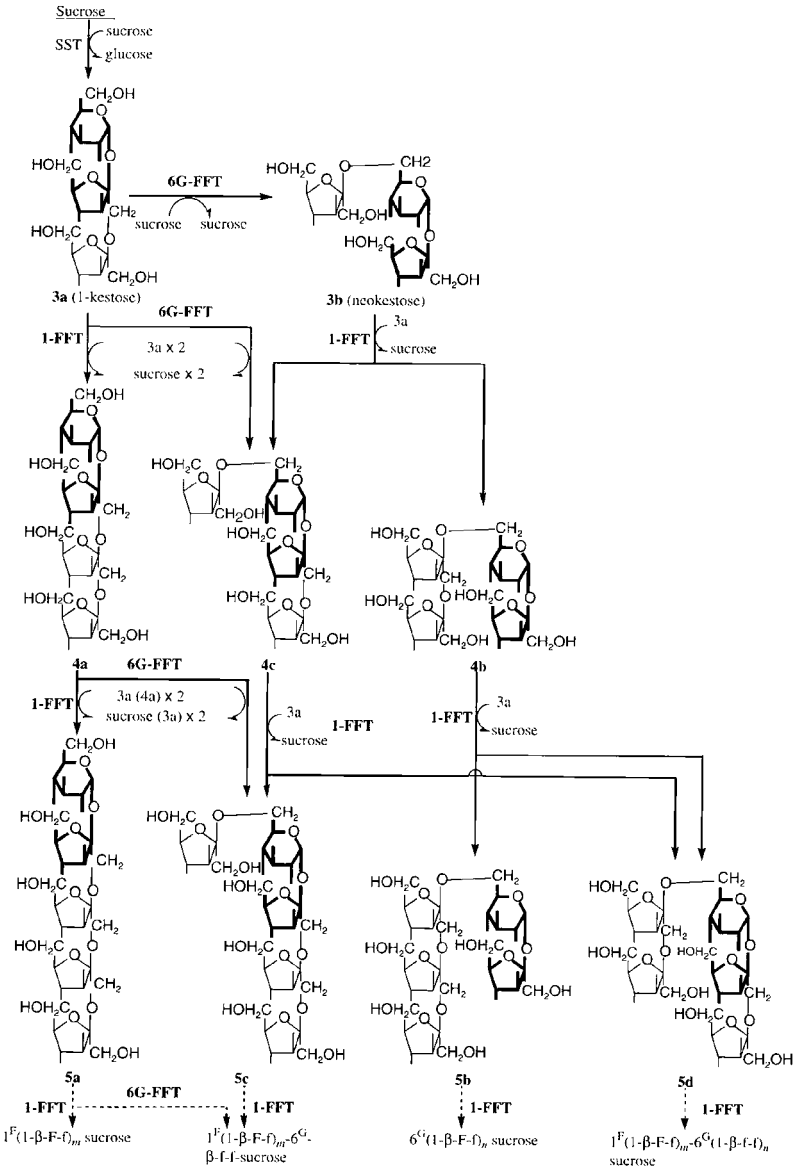


Fig. 8.5. The pathway of enzymatic synthesis of fructo-oligosaccharides in onion bulbs. The enzymes indicated are: SST, Sucrose:sucrose 1-fructosyl transferase; 1-FFT, fructan:fructan 1-fructosyl transferase; 6G-FFT, fructan:fructan 6^G-fructosyl transferase. Alternative and more explicit names for kestose and neokestose mentioned near the top of the diagram are 1^F-fructosyl sucrose and 6^G-fructosyl sucrose, respectively (from Fujishima *et al.*, 2005. Courtesy of *New Phytologist*©, 2005).

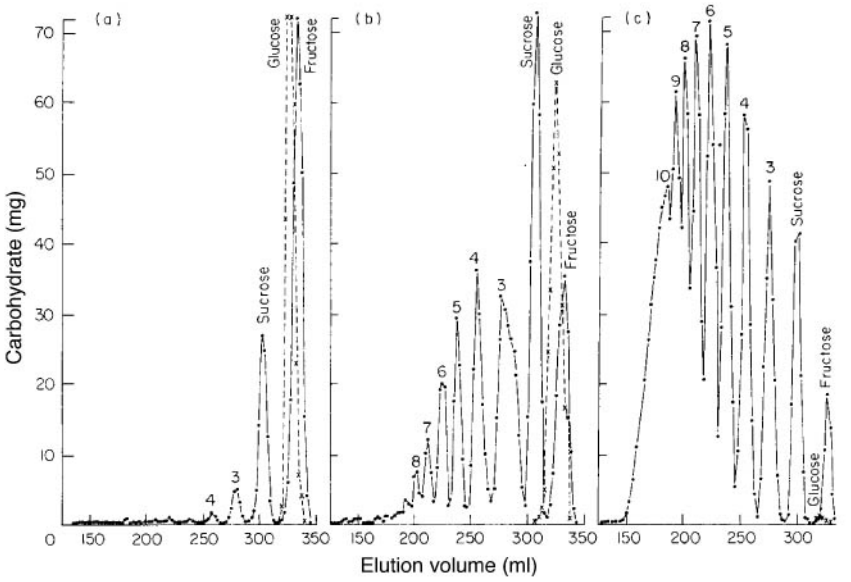


Fig. 8.6. A gel permeation chromatography separation of the non-structural carbohydrates from bulbs of onion cultivars varying in dry matter (DM) percentage. (a) Cv. 'White Spanish', 7.5% DM. (b) Cv. 'Australian Brown', 10.6% DM. (c) 'White Creole' × 'Southport White Globe' cross, 17.2% DM. Numbers on the peaks indicate the degree of polymerization of the fructans (from Darbyshire and Henry, 1979. Courtesy of the *Journal of the Science of Food and Agriculture*).

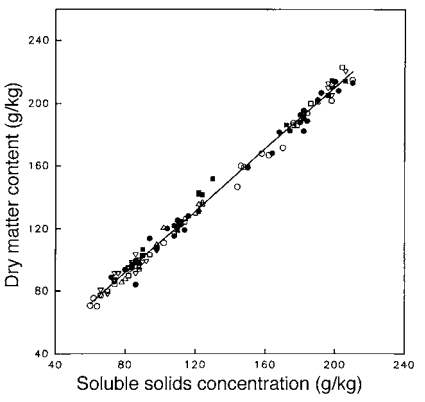


Fig. 8.7. The relationship between the dry matter content of bulb tissue and the soluble solids concentration – as determined by refractometer and expressed as sucrose equivalents – of bulb juice from 127 samples taken from 49 cultivars of onion (from Sinclair *et al.*, 1995a. Courtesy of the *Journal of the Science of Food and Agriculture*).

name implies, joining additional fructose units via the 2 position in their ring structure to the 6 position in the glucose ring in a fructo-oligosaccharide, the enzyme fructan:fructan 6^G-fructosyl transferase (6 G-FFT) can also catalyse the joining of the 2 position of a fructose unit to the 1 position of a fructose unit in a fructo-oligosaccharide, acting thereby as a fructan:fructan 1-fructosyl transferase (1F- FFT). The ratio of the 6G- FFT activity to the 1-FFT activity of the purified enzyme is 2.3:1 (Fujishima *et al.*, 2005). Therefore with just two enzymes, SST and the FFT, the range of fructo-oligosaccharides found in onion are synthesized, as shown in Fig. 8.5 (Ritsema *et al.*, 2004; Fujishima *et al.*, 2005). Hydrolytic enzymes that reverse these processes and degrade fructans by removing and releasing the terminal fructose unit have also been extracted from onions (Benkeblia *et al.*, 2004).

The sequence of amino acids making up the active site of the FFT enzyme has been determined (Ritsema *et al.*, 2004; Fujishima *et al.*, 2005). This is leading towards knowledge of the three-dimensional structure of the active site of the enzyme, which will clarify how it binds and catalyses in fructo-oligosaccharide synthesis (Ritsema *et al.*, 2004).

The gene for onion 6 G-FFT has been transferred to make transgenic chicory plants (Vijn and Smeekens, 1999) and a transgenic line of tobacco cells (Ritsema *et al.*, 2003), both of which synthesized the fructo-oligosaccharides found in onion. Thus using alliums, and also other fructan-accumulating species, the technology is developing to enable the synthesis of defined fructans in transgenic plants. It will be possible to synthesize, for example, onion-type fructo-oligosaccharides in sugarbeet, a plant that lacks fructose-hydrolysing enzymes, and therefore does not degrade any accumulated fructan. This could be a useful technology for producing particular fructans required for industrial purposes (Vijn and Smeekens, 1999).

The physiological function of fructans in plants is not fully understood. They and the FFT enzymes occur in the cell vacuole, and fructans are synthesized there. Clearly, they can act as reserve carbohydrates and also, by varying the DP, the osmotic effect of a given number of fructose units can be varied. For example, in a study using a range of onion cultivars, cell osmotic potential declined from –0.97 MPa to –1.41 Mpa as bulb percentage dry matter increased from 6.3 to 22.7%, much less rapidly than if the increased dry matter had been in the form of free fructose or sucrose (Sinclair *et al.*, 1995b).

Fructan-accumulating species are abundant in temperate climate zones with seasonal drought or frost, and almost absent in tropical regions. Fructan production and mobilization are less sensitive to low temperature than starch metabolism. The mobilization of fructan reserves for rapid expansion growth when temperatures rise in the spring, as in onion or garlic bulb sprouting, was an important factor favouring the evolution of fructan accumulation (Vijn and Smeekens, 1999). There is also evidence that fructan accumulation bestows resistance to drought and cold stress (Vijn and Smeekens, 1999). There are numerous reports that the fructan level in onion bulbs declines

during long-term storage (Hansen *et al.*, 1999; Benkeblia *et al.*, 2004) as fructans in bulb-scales are converted to fructose and sucrose and these are translocated to the bulb base plate to drive sprout growth (Pak *et al.*, 1995; see Chapter 7). Fructans accumulate transiently during seed development in onions, but do not ultimately form a significant seed reserve (Pollock and Lloyd, 1994).

The enzymes for fructan synthesis can be rapidly induced in onions; for example, when onion leaves were given 5% sucrose in the light, they started to accumulate the m-RNA to synthesize 1-SST after 4 h and the m-RNA for 6 G-FFT after 12 h, and 1-kestose and neokestose were also detectable after 4 and 12 h, respectively, indicating activity of 1-SST and 6 G-FFT enzymes at these time points (Vijn *et al.*, 1998). Transfer of onion plants from short to long photoperiods or from a non-inductive to inductive light qualities (730:660 nm ratio, see Chapter 4) induces a rapid increase in fructans in leaves and leaf bases up to 10 days before increases in bulbing ratio are visible (Darbyshire and Steer, 1990; Kahane *et al.*, 2001). The hydrolysis of some of the accumulated fructans may subsequently drive the expansion of outer leaf bases to give visible bulbing (Darbyshire and Steer, 1990).

The utility of fructans

The soluble carbohydrates in edible alliums are an important determinant of their qualities as foodstuffs. For the production of dried onion products – for example, onion powder or flakes, which are widely used in cooking and food manufacture – a high dry matter content of the bulb is required, as this reduces the energy required for evaporating water per unit of dried material. Also, bulbs for dehydration should have low quantities of reducing sugars (free glucose and fructose), since these can cause non-enzymatic browning reactions, resulting in an undesirable darkening of the dried product.

Fructan oligosaccharides have some sweetness that decreases with DP, and also water-binding and gelling properties that increase with DP. The latter properties make them useful as a fat substitute and as an ingredient in manufactured soups or sauces. Shallots, which typically contain 20% dry matter, have large amounts of fructans of DP 8–14 (Ernst *et al.*, 1998) and are regarded as ideal for making savoury sauces in French cuisine. Fructans are largely resistant to hydrolytic enzymes in the human intestinal tract. β1–2 fructan links are completely resistant to digestive enzymes, but β2–6-linked fructans may be partially hydrolysed (Delzenne, 2003). Therefore, they can impart many desirable qualities to food yet have a low nutritional energy content, and hence they are of great interest to food manufacturers.

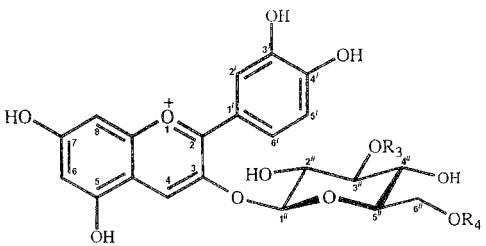
FLAVONOIDS

Two types of flavonoids are of particular interest in alliums; these are the anthocyanins responsible for the colour in red-skinned onion cultivars and the flavonols, which give a yellowish hue to onion flesh and are important precursors for yellow and brown skin pigments (see Chapters 3, 'Genetics' and 7, 'The Curing of Onion Skins').

Anthocyanins

Anthocyanins are red, purple or blue pigments found in many flowers and fruits. They all have the same basic central chemical ring structure, with the different groups attached to that ring causing their colour to vary (Salisbury and Ross, 1991). Anthocyanins have sugar groups (usually glucose) attached to certain positions on the core ring (see Fig. 8.8).

This core ring – minus attached sugar groups, i.e. after hydrolysis – is termed an anthocyanidin. The predominant anthocyanidin in red onions is cyanidin. There are also some reports of traces of peonidin and pelargonidin. The glucosyl group attached at position 3 in onion cyanidins may itself have various side groups attached. Figure 8.8 shows the predominant configurations found in European and North American red cultivars (Fossen *et al.*, 1996; Donner *et al.*, 1997). Anthocyanins constitute 0.11–0.22% of the dry weight of bulbs of red North American onion cultivars (Donner *et al.*, 1997). Cyanidin is also the predominant anthocyanidin in red shallots and *A. wakegi* (Arifin *et al.*, 1999) and in top onion, *A. altaicum* and chives (Fossen *et al.*, 1996).



Group attached to ring structure at: R_3	R_4	Name of Pigment	Total anthocyanins (%) (averaged over bulbs of three red cvs)
H	H	cyanidin 3-glc	13
glucosyl	H	cyanidin 3-(3^{6}glc glc)	2
malonyl	H	cyanidin 3-(3^{6}malonyl glc)	< 1
H	malonyl	cyanidin 3-(6^{6}malonyl-3^{6}-glc)	61
glucosyl	malonyl	cyanidin 3-(6^{6}malonyl- 3^{6}glc glc)	17
malonyl	malonyl	cyanidin 3-(3^{6},6^{6}dimalonyl glc)	4

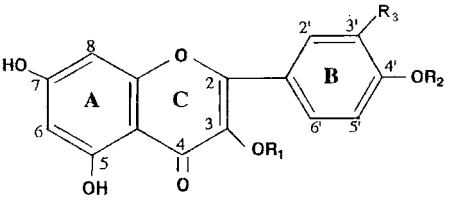
Fig. 8.8. The main anthocyanin pigments found in the bulbs of three red onion cultivars (glc, glucose) (from Fossen *et al.*, 1996).

Flavonols

Flavonols have a similar core ring structure to the anthocyanins and follow the same ring-numbering system to denote where side groups are attached. They are also normally linked to sugar groups to form glycosides within allium plants. The most important flavonol in onions and shallots is quercetin, while in leek and chive kaempferol is more common (see Fig. 8.9).

These flavonols are antioxidants and they can be ingested into the bloodstream, hence there is much interest in their potential health benefits (see below). Fenwick and Hanley (1990a) show 14 flavonols that have been found in edible alliums differing in how many and which sugar groups are linked to the core quercetin or kaempferol ring, and at which points they are linked. Glucose is by far the most frequently occurring attached sugar. Flavonols absorb ultra-violet light and they tend to occur in greater concentration in the surface cells of plants. Their synthesis is stimulated by light, and they probably have a role in minimizing cellular damage from ultra-violet light.

Onion bulbs, particularly red and yellow varieties, have very high contents of quercetin compared with other vegetables (about 350 mg/kg fresh weight). This is three times their nearest rival, kale, and nine times the next most abundant rival, French beans, and several orders of magnitude more than



Flavonol	*Group at R_1*	*Group at R_2*	*Group at R_3*
Quercetin	H	H	OH
Kaempferol	H	H	H
Isoquercetin	Glucose	H	OH
Quercetin 4′ monoglucoside	H	Glucose	OH
Quercetin 3,4′ diglucoside	Glucose	Glucose	OH

Fig. 8.9. The structure and names of the flavonol pigments found in onion bulbs (from Hirota *et al.*, 1998).

most others (Hertog *et al.*, 1992). The quercetin content of onion remains high even after chopping and boiling (Hirota *et al.*, 1998; Makris and Rossiter, 2001).

In living onion cells, nearly all quercetin exists combined with either one or two glucose units, as quercetin 4-glucoside or quercetin 3, 4-diglucoside (see Fig. 8.9) (Hirota *et al.*, 1998). Concentrations reported in the edible rings of red onion cultivars range from about 0.3 (Price and Rhodes, 1997) to 1.4% (Patil and Pike, 1995); weights were expressed as quercetin free of any attached glucose. Quercetin concentrations are higher in the outer scales of the bulbs, towards the top of each scale and in the abaxial (outward facing) epidermis of each scale (Patil and Pike, 1995; Hirota *et al.*, 1998). Concentrations are highest in red cultivars, about 50% lower in the yellow cultivars and about 99.7% lower in white cultivars. The dry skin of a red cultivar can have 3% of its dry weight as quercetin, of which 2% can be free (non-glucosides) (Patil and Pike, 1995).

During the senescence and drying of onion outer scales as they are curing to form the dry outer tunic of the bulb, flavonols are converted to various phenolic compounds, some of which condense to form brown pigments (see Chapter 7, 'The Curing of Onion Skins').

Other chemical constituents

Alliums contain the nutritive substances normally associated with vegetables. They also contain a number of other complex biochemicals in addition to their prominent flavour compounds and carbohydrates. The chemical composition of alliums was reviewed by Fenwick and Hanley (1985a, 1990a), and the following remarks are based on those reports.

The dry matter content of allium vegetables is usually in the range 7–15%, with leafy shoots usually a percentage point or two lower in dry matter than bulbs. Garlic bulbs are the exception, ranging in dry matter content from 30 to 56%, depending on cultivar. On a fresh-weight basis these vegetables typically contain 1–2% protein, around 0.2% fats and 5–12% carbohydrates, the latter depending very much on dry matter content which, with onion bulbs and garlic bulbs, can vary greatly with cultivar, as discussed previously. Protein contents of garlic bulbs of 4–6% are common, in accord with their high total dry matter content. The ash content of vegetable alliums is typically 0.6–1.0%, the higher values again being associated with higher dry matter percentages. Typically, their calorific value is around 35 calories/100 g, but is around 140 for garlic bulbs.

A number of phenolic substances have been isolated from alliums, in addition to protocatechuic acid from the outer skins of onion bulbs, as discussed in Chapter 7, 'The Curing of Onion Skins'. Most of the amino acids commonly found in proteins have been detected in onions and Japanese bunching onion. They contain

relatively large amounts of arginine and glutamic acid, and these may be important N reserves. Onion skins contain large amounts of pectin and are suitable sources for the extraction of pectic substances for processing (see 'Onion Waste Processing', below). A number of sterols and saponins have been extracted including, from leek leaves, aginosid, a steroidal saponin that exhibits growth inhibitory activity against leek moth (see Chapter 5). Several other complex chemical structures have been isolated from alliums, including prostaglandins.

MEDICINAL EFFECTS OF ALLIUMS

Introduction

The study of the health benefits of alliums is a burgeoning field of research, to which whole books have already been devoted (e.g. Koch and Lawson, 1996). The subject is complex because it involves the interaction of pharmacologically active compounds from alliums with the intricate biochemistry and physiology of human disease. Moreover, as mentioned above, pharmacologically active substances derived from ACSOs are chemically complex and can be unstable and short-lived, and their quantity and nature depends on the chemical environment during and subsequent to the alliinase reaction that releases them (Block, 1992).

However, the subject is exciting, because alliums and the substances derived from them are therapeutic for many of the diseases of affluent societies, notably heart disease (arteriosclerosis), cancer, asthma and diabetes, as well as having powerful anti-microbial properties for countering infectious diseases. Medicinal effects have been reviewed by Fenwick and Hanley (1985a), Augusti (1990), Koch and Lawson (1996), Griffiths *et al.* (2002), Keusgen (2002) and several authors in Guangshu (2005).

Alliums have a long history of medicinal use and are ascribed to curing of a wide range of ailments in traditional medical writings. Scientific studies have shown considerable pharmacological effects that have, in some cases, been attributable to specific molecular structures, mostly derived from the flavour-inducing sulfur compounds discussed above. Herein is a brief review of the subject, with an indication of the therapeutically active compounds present in alliums, and some striking examples of research findings at different levels of organization, ranging from molecular pharmacology to human epidemiology, that together are building up evidence for benefit to health from alliums.

Four types of compound found within alliums are of therapeutic interest. First are the substances derived from ACSOs that are largely responsible for flavour and pungency. Second are the flavonoids, including quercetin, which is a powerful antioxidant and which is found in higher concentration in onion than in any other vegetable or fruit. Third there are the fructo-oligosaccharides and fructans, soluble but non-digestible carbohydrates that promote a health-

beneficial microbial flora in the lower digestive tract. Finally, alliums can substitute selenium for sulfur absorption in selenium-rich soils and, being rich in sulfur-containing substances as well as widely consumed, they may be useful for increasing dietary selenium intake, which would be beneficial to health in regions like the UK, where mean selenium intake is low.

Examples from different types of research indicating health benefits

Epidemiology

1. Comparisons on adherents to Jainism in India, who either abstain from eating onions and garlic, eat moderate amounts (< 200 g of onion, < 10 g of garlic per week) or eat large amounts (> 600 g onion, > 50 g garlic per week), showed that the allium eaters showed: (i) less tendency to form blood clots; and (ii) lower levels of cholesterol and the lipoproteins associated with heart disease in their blood serum than the abstainers.
2. In Jiangsu province, China, where oesophageal and stomach cancer are common, the intake of allium vegetables was found to protect against these cancers.
3. A strong inverse association between the onion consumption and the occurrence of stomach cancer was found in a large survey of diet and cancer from The Netherlands.

Clinical interventions

1. Adult volunteers suffering from allergic bronchial asthma were treated with a dilute ethanol extract of sliced onions before being exposed to an inhaled allergen. The asthmatic reactions in the bronchi were markedly reduced.
2. Administration of garlic powder improved peripheral arterial circulation in patients diseased in this respect and improved their walking. In a separate study, garlic powder improved subcutaneous microcirculation in healthy subjects.
3. Administration of garlic or garlic extracts to patients with high blood cholesterol resulted in a 10–15% reduction, a similar effect to prescribing a near cholesterol-free diet.

Animal studies

1. In guinea pigs with induced bronchial constrictions analogous to asthma, oral treatment with freeze-dried onion juice counteracted the constrictions. Thiosulfinates and cepaenes were the active compounds.
2. Garlic powder reduced blood cholesterol, lipids and blood pressure in rats with high cholesterol.

3. Raw extracts of *A. fistulosum* lowered systolic blood pressure and prolonged bleed times in rats, possibly by suppression of platelet aggregation in blood clotting.
4. Mice inoculated with bladder cancer cells and then provided with 500 mg garlic/100 ml of drinking water showed significant reductions in tumour volume and mortality over controls.

Cellular and biochemical studies

1. The most widely reported pharmacological effect of alliums and extracts from them is their inhibition of the aggregation of blood platelets. Platelet aggregation occurs in blood clot formation and can cause thrombosis. Substances in alliums are therefore powerful anti-thrombotics. Very low concentrations of the compounds ajoene from garlic and cepaenes from onions (see Fig. 8.4) can inhibit platelet aggregation.
2. Studies using rat and human liver cells have shown precisely which points in the biosynthetic pathway of cholesterol are inhibited by which substances from garlic (Gebhardt and Beck, 1996; Keusgen, 2002). Allicin inhibits three enzymes in the pathway, ajoene two of the same enzymes and diallyl disulfide one of the enzymes. Diallyl disulfide also induces a higher level of cyclic adenosine monophosphate (cAMP), which leads to more of the inactive phosphorylated form of two enzymes early in the biosynthetic pathways of cholesterol and fatty acid synthesis. Concentrations of 0.5 mM allicin or ajoene caused a 30% decrease in cholesterol biosynthesis; this is medically more desirable than a total inhibition. Clearly, the action of garlic in this process is complex, and different forms of garlic (fresh or extracted) that contain different active compounds all have cholesterol-lowering potential.

In contrast to these positive results, there are other studies showing no benefits from alliums or substances derived from them on aspects of disease. For example, a randomized study on adults with moderately elevated cholesterol found no benefit in terms of reduced cholesterol of consuming an average-sized (4 g) garlic clove, or its equivalent as garlic powder or extract, daily for 6 months (Gardner *et al.*, 2007). The reasons for conflicting reports are not clear, although the amounts of allium ingested may be a factor. The latter study involved eating only moderate amounts of garlic that could be part of a normal diet for many people.

Antioxidants and the prevention of free radical damage

The oxidative breakdown of food that provides metabolic energy for all aerobic organisms, including humans, produces as an undesirable by-product certain highly reactive groups with an unpaired outer electron, variously known as

free radicals, reactive oxygen species or superoxides. These reactive groups have the capacity to attack and damage many vital biochemical systems, including DNA molecules. Such damage is thought to initiate many degenerative diseases, including arterial disease, and a proportion of such DNA damage can lead to loss of control over cell division, resulting in a proliferation of cancer cells. The ageing process is also regarded as being largely a result of cumulative damage from free radical attack.

Alliums, in common with other vegetables, are a rich source of antioxidants that are capable of reacting with free radicals and chemically neutralizing them. In particular, quercetin, of which onion is the richest vegetable source, is a potent antioxidant that can raise the overall antioxidant level in blood plasma following ingestion. Twenty to 50% of ingested quercetin glycosides are absorbed, depending on the glycoside type (see Fig. 8.9), and this also affects absorption time, which ranges from 0.5 to 9.0 h. Subsequent excretion of quercetin is slow, with a half-life of about 24 h. Ability to trap certain types of free radicals has also been demonstrated in some compounds derived from garlic – for example, diallyl disulfide (DADS). The more antioxidant present in the system the greater the proportion of free radicals that can be neutralized before they cause cellular damage.

In addition to ingested antioxidants, cells produce their own enzymic systems for neutralizing free radicals and certain mineral elements – notably, selenium, iron, manganese and copper – are essential cofactors for these enzymes. Hence the mineral content – in particular, the selenium content of vegetables – is important to this aspect of cellular defence against free radicals and their cancerous potential.

It is inevitable that some carcinogens enter the cell biochemistry. Compounds from alliums have been shown to suppress enzymes involved in carcinogen activation (termed the Phase I enzymes) and to induce or up-regulate enzymes involved in detoxification of carcinogens (termed the Phase II enzymes). For example, allicin and diallyl disulfide inactivates the human cytochrome P450 involved in carcinogen activation *in vitro*. Furthermore, rats fed garlic powder had decreased activation of the carcinogen aflatoxin and increased levels of the enzymes involved in its detoxification in their livers, and showed less genetic damage as a result of ingesting carcinogens than controls (Guyonet *et al.*, 2002).

The Phase II enzymes combine carcinogens with biochemical groups that favour their excretion in urine. Most Phase II enzymes – including glutathione reductase and quinone reductase – are up-regulated by feeding diallyl disulfide, which is found in garlic or garlic oil. Garlic or garlic oil and onion oil have been shown to decrease the number and rate of development of tumours in mice and to suppress the growth of leukaemia cell cultures (Griffiths *et al.*, 2002).

Health benefits of fructans

Since fructans largely escape digestion in the upper intestine, they are an important source of energy for bacteria that produce β fructosidases in the caeco-colon. This leads to a proliferation of beneficial bacteria like *Bifidobacteria* and *Lactobacilli* to the detriment of harmful bacteria. These health-beneficial bacteria have been termed 'probiotic' bacteria, and products containing them are widely sold as dietary supplements. The proliferation of probiotic bacteria favoured by fructans has been termed the 'prebiotic effect' of fructans (Delzenne, 2003). These effects result in a colonic microbiota that produces short-chain fatty acids there (e.g. lactate and butyrate). This results in a lower pH that in turn favours increased absorption of mineral cations from the gut into the bloodstream. The short-chain fatty acids produced can be absorbed and reach the liver and modify lipid metabolism, with consequences for lipids circulating in the blood that include reductions in total and LDL cholesterol.

The changes in colonic bacteria may reduce carcinogen activation in the colon and stimulate the immune system, leading to improved resistance to infection and cancer resistance – in particular, but not exclusively, to colonic cancer. Benefits for glucose metabolism – including increased insulin secretion and changes in hormone metabolism – have also been reported in animal studies on fructans. So, the benefits for health of ingestion of non-digestible oligosaccharides like fructans are multifaceted and are systemic; they are not confined solely to effects in the digestive tract (Delzenne, 2003). The mechanisms for these effects are far from fully understood, but they are yet another aspect of the health-promoting benefits of edible alliums that are earning them a reputation as 'functional foods' of particular importance in counteracting the diet-related diseases of affluent societies.

Selenium and alliums

The mineral element selenium (Se) is known to be involved in the prevention of cardiovascular disease, the stimulation of immune responses, the suppression of inflammatory conditions, brain function, reproductive physiology and the prevention of cancer, particularly prostrate cancer in men. The mean dietary intake of Se in much of Europe is only about 60% of the recommended daily amount (RDA) in the USA. Current research indicates that an intake of about 200 μg/day gives maximal benefits to health, about three times the current RDA in the USA. Hence, there is interest in supplementing dietary Se intake in some countries.

Selenium is chemically similar to sulfur, being adjacent to it in Group 6 of the periodic table. It is absorbed and incorporated into flavour compounds by onions in a parallel fashion to sulfur. It is quite feasible to supply the Se RDA in a single daily serving of onions grown in Se-enriched soil. Moreover, onions are

widely consumed and are major ingredients in many pre-prepared foods, so that they offer the opportunity to enrich the Se intake of a large proportion of the population without the need to change eating habits (Griffiths *et al.*, 2002). It is also known that consumption of excessive Se, perhaps as low as 600 μg/day, is harmful, so supplementing Se intake via vegetables – which tend to self-regulate their content of Se and other micronutrients – is probably safer than recommending that people take Se directly as diet-supplementing pills.

In addition to onions, Se-enriched garlic has been studied as a potential 'functional food' for health enhancement (Block, 2005). The deliberate enrichment and utilization of Se-enriched alliums is still in the early phase of research and remains just a possibility for the future; this may be taken up alone, or in parallel with Se enrichment of other crops (e.g. bread-making wheat).

Conclusions

It seems that benefits to health deriving from alliums are manifold and multi-faceted, although efficacy studies have not always shown benefits. Evidence for positive effects on health is accumulating from studies ranging from biochemical reaction chemistry to population epidemiology. All four major categories of therapeutic substances from alliums – namely, flavour compounds, antioxidants, fructans and selenium – act against several major classes of disease. Studies show that a single biochemical, e.g. ajoene, can be active at several points in a biochemical pathway of consequence to disease and can also be active in several different such pathways of consequence to different diseases.

Research is continuing to refine our understanding of these processes and to pinpoint more precisely which compounds and which enzymes and biochemical pathways are involved. In addition, we could have benefits of not just one of the therapeutic compounds in alliums but from the combination of compounds from all four categories of therapeutic substance. It is possible that there are synergistic effects between the many compounds found in alliums so that, acting together, they give health benefits beyond those ascribable to single compounds. It is important to remember that the mechanisms for health benefits of different alliums may not be the same, since the types and amounts of flavour compounds, fructans and flavonols differ between species and even between cultivars.

It seems rarely asked why substances in alliums (and other vegetables) are beneficial to health. We have seen that flavour compounds are likely to be involved in chemical defence against pathogens and pests, and this must involve interaction with, and disruption of, the invaders' biochemistries. It maybe just fortuitous that alliums, in evolving their chemical defences, have evolved substances that act as medicines in humans. The effects on humans of ingesting the secondary metabolites and endogenous pesticides in crops are by

no means always wholly benign, and may depend on the quantities ingested (Trewavas and Stewart, 2003). Therefore, we must be open to the possibility of negative effects as well positive benefits to health. There are few reports of disbenefits from alliums, apart from the introduction of unwanted taint or flavour into milk from cows eating them.

Partly because of the multiple aspects of the potential health benefits, it is difficult, if not impossible, to make specific, predictive, quantitative and universally true statements on this subject. There remains, therefore, much potential for further research to clarify this subject. It is clearly a complex field, but we can say with certainty to those that grow and market allium vegetables that these have great potential for prevention and even cure of many of the diseases prevalent in modern societies. The message to consumers is simple: just eat plenty of alliums (and other vegetables) for your health's sake.

PROCESSED PRODUCTS FROM ALLIUMS

Introduction

A number of manufactured products are produced from alliums for use in cooking, the formulation of processed food or as medicines. The utilization of alliums in food manufacture has been reviewed by Fenwick and Hanley (1990b), and will only be outlined briefly here. The flavour of processed onion and garlic products is generally rather weaker than an equivalent quantity of the fresh product. Also, the flavour is somewhat different from the fresh product. Loss of flavour can result from the rapid destruction of the alliinase enzyme during processing, or from the destruction of flavour precursors. The composition and spectrum of the flavour-determining volatiles derived from onions or garlic depends very much on the temperature, timing and duration of various cooking and manufacturing processes (Lancaster and Boland, 1990). An increasing volume of allium vegetables are being sold as partially processed fresh produce, either alone or in mixed packs with other produce. The section on 'Green Onion Storage' in Chapter 7 describes aspects of this technology.

Concentrated flavour oils

Concentrated oils can be used to impart the flavour of onions or garlic to processed foods without the difficulties of handling a large bulk of fresh bulbs. Onion oil and garlic oil are produced by boiling a mixture of the minced bulbs after allowing it to stand for several hours and extracting the oils from the condensed steam, a process known as steam distillation. Yields of 0.002–0.030 g of onion oil/100 g of fresh bulbs, or 0.10–0.25 g of garlic oil/100 g of fresh bulbs, are obtained.

Recently, industrial techniques for extracting the aromatic flavour constituents from unheated homogenates of bulbs have been developed. The oil-soluble aromatics are extracted into food-grade solvents, and this can then be evaporated to concentrate the flavour substances and recover the solvent. Because these aromatic oils are so concentrated, they are sometimes dispersed into a solid phase using salt, dextrose or flours as a carrier. Alternatively, they can be micro-encapsulated using edible polymers, e.g. gum arabic. These forms of dilution and dispersal simplify the mixing and incorporation of the flavour oils into manufactured foods.

Dehydrated products

Onions and garlic are widely used in dehydrated form. Onion varieties for dehydration should be white-fleshed and should have a high dry matter percentage. Suitable varieties include the well-known cvs 'Southport White Globe' and 'White Creole', bulbs of which contain 17–21% dry matter. The processing involves first washing the bulbs, removing the skin, roots and tops, surface sterilization by flame or alkali, washing and then slicing or chopping. The slices are dried in hot air, starting at 75°C and decreasing to 60°C in three stages as the moisture content decreases. Drying at too high a temperature causes darkening (caramelization). Hot-air drying is followed by a final drying to 4% moisture while the flakes are agitated in a blast of warm air. The production of dried garlic is very similar, except that a maximum drying temperature no higher than 60°C is necessary. Dried flakes may be further processed into powders.

Onion and garlic powder and flakes are widely used in manufactured soups, ketchups, sauces and mayonnaises. For use in catering, onion or garlic powder may be blended with 70–80% salt plus 1–2% calcium stearate to produce onion or garlic 'salt'. The dehydrated products may be incorporated in more elaborate pre-prepared foods. For example, onion 'rings' suitable for deep frying or selling cooked and packed as a snack food are produced by extruding a paste containing dried onion. Dehydrated green onions, leeks and chives are also produced. The best-quality dehydrated chives are produced by freeze-drying the chopped leaves under reduced atmospheric pressure, followed by packing in nitrogen-flushed polyethylene bags (Poulsen, 1990).

Pickles

In many countries pickled allium bulbs are eaten in large amounts. Onions for pickling are either common, yellow–brown-skinned varieties or special white 'silverskin' types. Small bulbs, suitable for pickling, are produced by growing at a high plant density (see Figs 6.7 and 6.8). Onions for pickling are first peeled,

then allowed to ferment in 10% brine for 24–96 h. During fermentation, sugars in the bulbs are converted to lactic acid plus small amounts of acetic acid and alcohol. The fermentation is controlled by adding small quantities of lactic acid. A decrease in pH to < 4.6 in the bulbs within a few days prevents the growth of botulism bacteria. The pickled bulbs are bottled in vinegar, possibly darkened with caramel and pasteurized at 80°C. In Japan, bulbs of rakkyo are similarly pickled in brine and then bottled in vinegar plus sugar to make sweet pickle, or vinegar plus salt to make a sour pickle (Toyama and Wakamiya, 1990).

Onion waste processing

In Europe, 450,000 t of onion waste consisting of brown skins and outer fleshy scales are produced annually from the industrial processing of onions. This material is not suitable for animal fodder because of its strong taste and it also carries the risk of spreading crop disease – for example, white rot (see Chapter 5). The waste may be transformable into a valuable source of pectic substances and dietary fibre-rich, food-grade products (see Chapter 7, 'The Skin of Onion Bulbs') using appropriate extraction and cooking techniques – for example, extrusion cooking (Ng *et al.*, 1999).

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